

ENGLISH EOCENE CRUSTACEA (LOBSTERS AND STOMATOPOD)

by W. J. QUAYLE

ABSTRACT. The Eocene lobsters from the London Clay, Bracklesham and Barton Beds are revised. Nine species of lobster are represented, three new, *Homarus morrissi*, *Hoploparia wardi*, and *H. victoriae*, belonging to six genera. *Trachysoma scabrum* Bell is placed in *Glyphea*. The remaining species, *H. gammaroides* M'Coy, *Archaeocarabus bowerbanki* M'Coy, *Limparus eocenicus* Woods, *L. scyllariformis* (Bell), and *Scyllarides tuberculatus* (König), are redescribed with further information. The stomatopod *Squilla wetherelli* Woodward is redescribed and placed in *Bathysquilla*.

IN 1849 M'Coy described three new species of lobster from the London Clay, *Hoploparia gamma-roides*, *H. belli*, and *Archaeocarabus bowerbanki*. In 1858 Bell described *Trachysoma scabrum*, new genus and species, and *Thenops scyllariformis*, new species, and redescribed *Scyllaridia koenigii*, first described by König (1825), as *Cancer (Scyllarus?) tuberculatus*; he also made additions to M'Coy's descriptions of *H. gammaroides*, *H. belli*, and *A. bowerbanki*. All of Bell's specimens came from the London Clay. Woods in his monograph of the Fossil Macrurous Crustacea of England (1925–1931) described *Limparus eocenicus*, a new species from the London Clay, and redescribed *H. gammaroides*, *A. bowerbanki*, *L. scyllariformis*, and *Scyllarides koenigii*; *H. belli* was relegated to synonymy. In a footnote on p. 94 he mentioned a large specimen of *Homarus* sp. from the Barton Beds of Hampshire, first mentioned by Gardner *et al.* (1888). On p. 73 he mentioned but did not describe the only known specimen of *Trachysoma scabrum* and figured it on pl. 22, fig. 1. Cooper (1974) listed the known records of the English Palaeogene decapod Crustacea up to that time.

Further collecting from some of the older sites, with some new ones, has added considerably to our knowledge of the English Eocene macrurous Crustacea.

STRATIGRAPHY

Some of the localities mentioned by the earlier authors are no longer available, though on rare occasions temporary exposures occur through road works and building. The following is a list of localities from which the specimens used in this work were obtained, either by the old collectors such as Bowerbank, Wetherell, Meyer, and Caleb Evans, or in recent years.

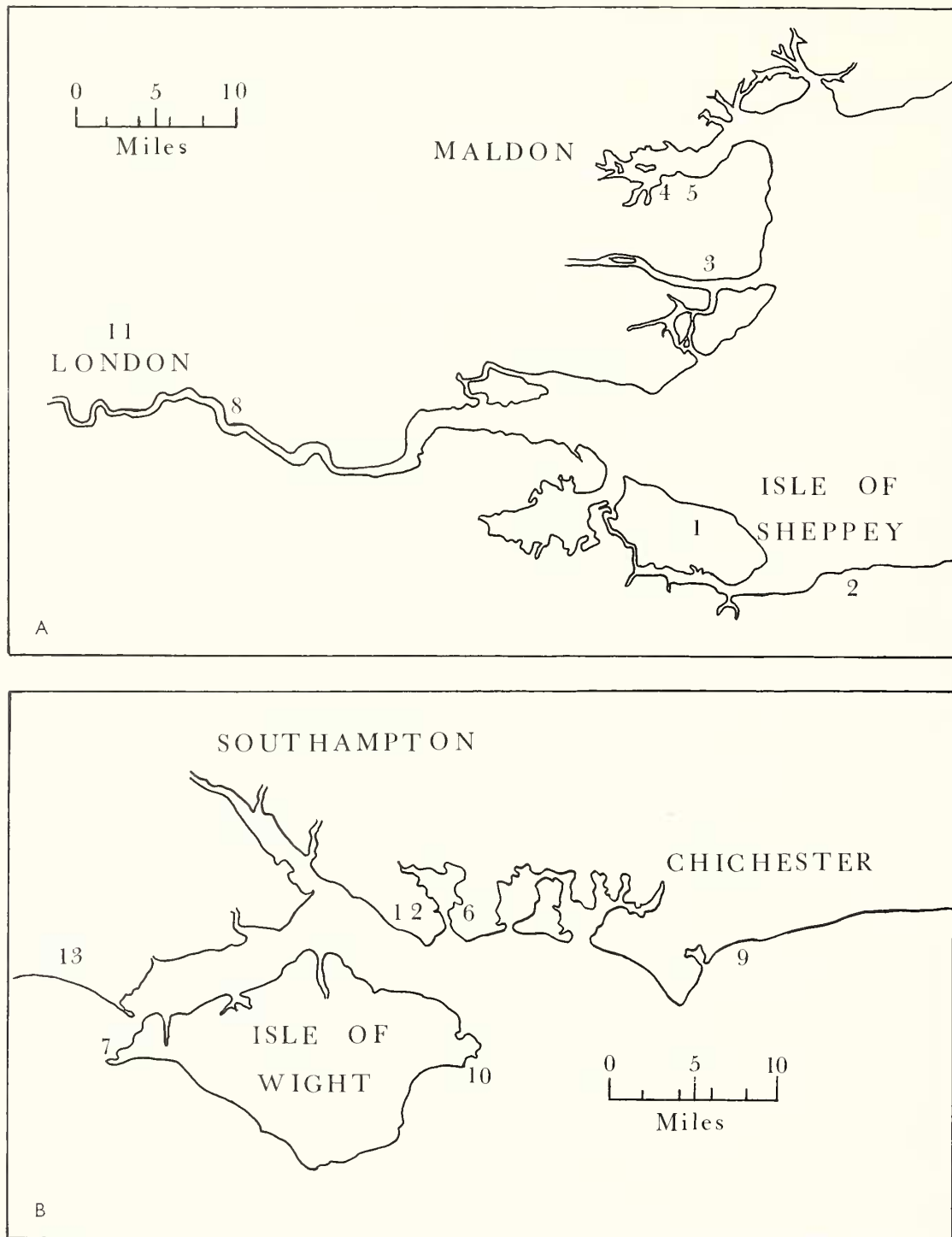
1. Isle of Sheppey, Kent; cliff and foreshore exposures, London Clay, Divisions C, D, and E (King 1981, 1984). Grid reference TQ 955 738–TR 024 717.

2. Herne Bay, Kent; Beltinge cliff, London Clay, Divisions A2, A3, and lower half of B (King 1981), TR 195 685. Cliffs are now landscaped, leaving a foreshore exposure of A2. Thanet Beds, TR 2051 6881 and TR 2046 6875, Units E and G (Ward 1979).

3. Burnham on Crouch, Essex; tidal river, with foreshore exposures, London Clay, Division D (King 1981), TQ 920 968–922 966.

4. Maylandsea, Essex (George and Vincent 1982, pp. 39–41); tidal river with foreshore exposures, London Clay, lower part of Division B (King 1981), TL 908 034–908 037.

5. Steeple, Essex (George and Vincent 1977, pp. 105–107); tidal river with foreshore exposures, London Clay, lower part of Division B (King 1981), TL 916 043.



TEXT-FIG. 1. Localities in A, the London Basin and B, the Hampshire Basin (see text for key to numbers).

6. Portsmouth Docks, Hampshire; former temporary exposure, 'Dockyard Extension Works'. The crustacean fauna (Woodward 1871, 1873) is similar to that of Whitecliff Bay. All the Crustacea came from the London Clay, the Dentalium Bed of Meyer (1871), in the upper part of Division B2 (King 1981).

7. Alum Bay, Isle of Wight, Hampshire; cliff exposure, London Clay, Divisions A, B, C, and D (King 1981), SZ 306 853.

8. Aveley, large quarries south-west of Aveley, Essex; London Clay, Divisions A, B, and C (King 1981), TQ 557 805 and 555 809. Working has now ceased. Material collected by R. J. Kirby is in the Oxford University Museum.

9. Bognor Regis, Sussex; foreshore exposure, London Clay, Divisions A to C, SZ 942 990-895 970.

10. Whitecliff Bay, Isle of Wight, Hampshire; cliff and foreshore exposures, Bracklesham Group, SZ 640 861. Crustacea found in a line of iron stained phosphatic nodules in the Wittering Division (Fishers Bed 1), approximately 7.5 m above the base of the Bracklesham Group. Some 75 % of the nodules collected *in situ* and others collected loose from the beach (probably from this horizon) had pieces or specimens of crustaceans. *Limuparus* is common, in association with *H. morrissi* sp. nov. A nodule in the Sedgwick Museum, C69620, collected by H. Keeping in 1887, and labelled Lower Bagshot Beds, is thought to have come from this horizon.

11. Various London Clay localities around London, now no longer available, i.e. Whetstone; Chalk Farm, Divisions B and C; Highgate, Division E (King 1981), and various motorway construction sites around London.

12. Lee-on-the-Solent, Hampshire; foreshore exposure, Elmore Formation (Kemp *et al.* 1979), Huntingbridge Division, Bracklesham Group, SU 569 500.

13. Barton Beds, Christchurch Bay; cliff with occasional foreshore exposures; stratigraphic horizons as in Burton (1929), SZ 199 928-261 923.

Repositories. Specimens prefixed BM are in the Palaeontological Department, British Museum (Natural History); SM, Sedgwick Museum, Cambridge; OUM, Oxford University Museum, Oxford; PE, Passmore Edwards Museum, London; JSQ, W. J. and S. Quayle Collection; JC, John Cooper Collection.

SYSTEMATIC PALAEOLOGY

Infraorder ASTACIDEA Latreille, 1803

Family NEPHROPIDAE Dana, 1852

Subfamily HOMARINAE Huxley, 1879

Genus HOMARUS Weber, 1795

Type species. *Cancer gammarus* Linné, 1758, Recent, European, by subsequent designation (Rathbun 1904, p. 170).

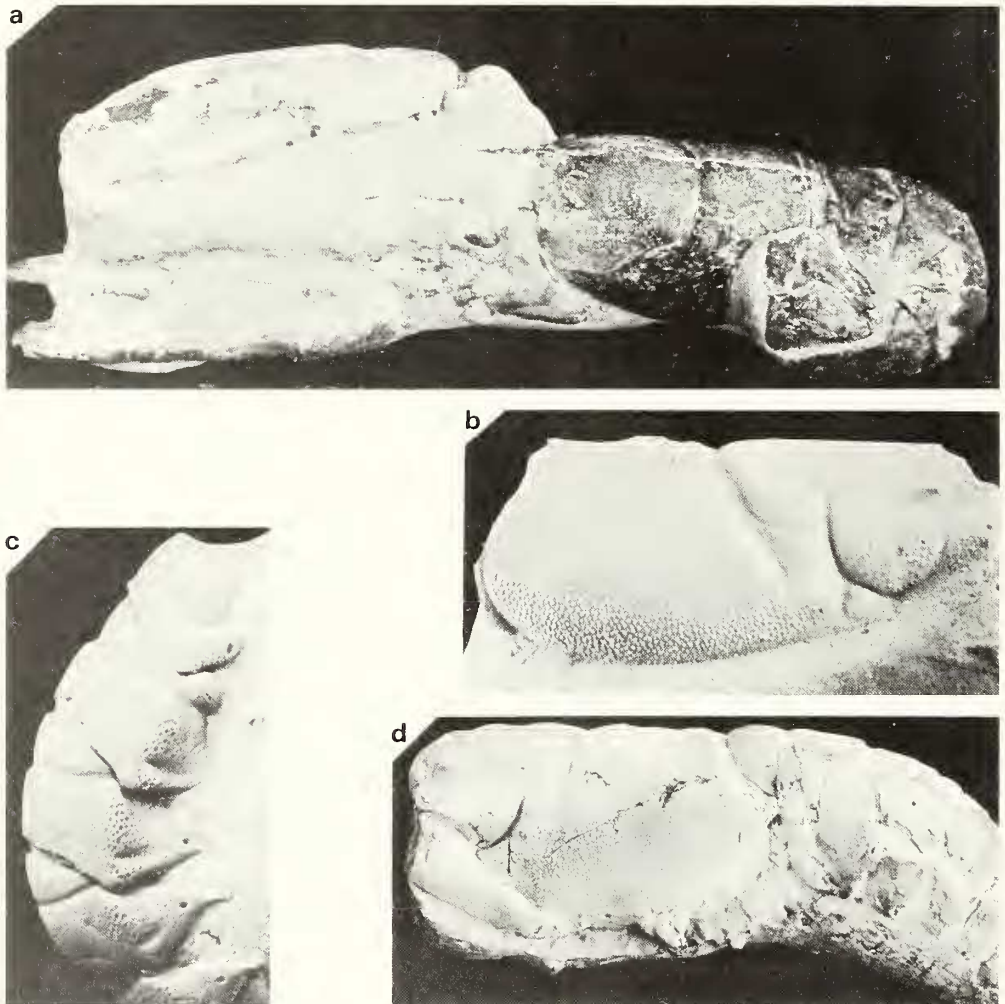
Diagnosis. Rostrum rather short and spiny, carapace without ridges or spines behind the suborbital spine, cervical groove clearly developed only below gastro-orbital groove, postcervical groove long and smoothly curved, connecting lowest part of cervical with posterior part of branchiocardiac groove; chelae stout, heterochelous.

Range. Cretaceous-Recent.

Discussion. Woods (1931) could find no generic distinction between the fossil forms of *Hoploparia* and the living species of *Homarus*. Stenzel (1945, p. 427) stated that eleven species of *Homarus* had been described from the Cretaceous of the United States east of the Rockies. These eleven are largely made up of specimens identified by Rathbun (1926*b*, 1935) as *Hoploparia*. Stenzel also described two new species, *Homarus brittonestrus* and *H. davisi*. These are similar to the living species of *Homarus* in the nature of the carapace grooves.

Glaessner (1969) whilst noting that 'the distinction between some of these species is difficult and disputed' maintained that a number of characters show that the genera are distinct. In *Homarus*: cervical groove clearly developed only below the gastro-orbital groove; postcervical groove long and curved, connecting the lowest part of the cervical groove with the posterior part of the branchio-cardiac groove; carapace without ridges or spines behind the suborbital spine. In *Hoploparia*: cervical groove developed above and below the gastro-orbital groove; postcervical distinct and connected with the cervical groove through a semicircle; carapace can have ridges or spines behind the suborbital spine.

There appear to be two distinct patterns of grooves. The first compares with the living forms of *Homarus* as depicted by Glaessner (1969, R461, fig. 1*b*) and Holthuis (1974, p. 816, fig. 24). The second is as for the fossil species of *Hoploparia* (text-fig. 4*A*).



TEXT-FIG. 2. *a*, *Homarus morrissi* sp. nov., London Clay, Soft Rock, Bognor Regis, holotype, BM In.63392, $\times 0.8$. *b*, *c*, *Hoploparia gammaroides* M'Coy, London Clay, Isle of Sheppey, lectotype, BM 46366. *b*, carapace, $\times 2$. *c*, somites one to five, $\times 2$. *d*, *H. wardi* sp. nov., London Clay, Isle of Sheppey, holotype, SM C19314, $\times 1.1$.

Homarus morrиси sp. nov.

Plate 64, figs. 5 and 7; text-figs. 2a and 3

- 1849 *Hoploparia gammaroides* M'Coy, p. 177.
 1850 *Astacus belli* (M'Coy); Dixon, pp. 114, 222, pl. 15, figs. 3 and 4.
 1858 *Hoploparia gammaroides* M'Coy; Bell, p. 38, pl. 8, figs. 5 and 6?; pl. 9.
 1980 *Hoploparia gammaroides* M'Coy; Morris, p. 9.

Derivation of name. After Mr S. F. Morris, Department of Palaeontology, British Museum (Natural History).

Types. Holotype: BM In.63392 (text-fig. 2a), collected by B. A. Williams (Venables 1971), London Clay, Soft Rock, Bognor Regis. Paratypes: BM In.35299, In.48223, In.48226, and In.48227 collected by E. M. Venables; BM In.63364 (Pl. 64, fig. 5), In.63365 (Pl. 64, fig. 7), collected by D. Bone; all from Soft Rock, London Clay, Bognor Regis, Sussex.

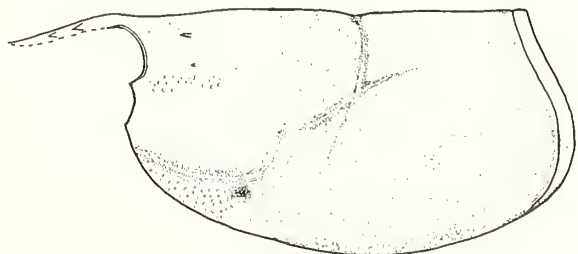
Diagnosis. A *Homarus* with fine grooves, with two rows of spines on the inner edge of the palm and a single spine on the outer margin at the base of the dactylus; carapace with fine pits.

Horizon and locality. London Clay: Soft Rock and the Beetle Bed, Bognor Regis; Isle of Sheppey: near Copenhagen House, London; Bracklesham Group, Bracklesham Bay, Selsey and Whitecliff Bay, Isle of Wight; Barton Beds, Christchurch Bay.

Description. *Cephalothorax.* Rostrum dentate, slightly less than half the length of the carapace; carapace with a postorbital spine and directly below this, a suborbital spine. The cervical groove starts almost level with the antennal base and drops down, curving to join the antennal groove. This runs almost straight to the front margin. The postcervical groove starts on the median line, slightly more than half the carapace length from the base of the rostrum. It drops almost straight down, then curves towards the front at a slight downwards angle and dies out. The postcervical is joined at the bend by the faint branchiocardiac groove running away towards the rear, another fine groove drops away at this point and runs parallel with the cervical groove for a short distance before dying out. Carapace with fine pitting. (Refer to text-fig. 4A for position of carapace grooves.)

Abdomen. On the second abdominal somite the pleuron is quadrate, the anterior angle rounded, and the posterior angle with a posterior pointing spine. Surfaces are smooth with fine pores; there is a large pit between the lateral and posterior margins before they join. Somites three to five have a transverse groove on the anterior third, extending to the boundary of the tergum at the anterior margin; pleura are triangular, falcate, with an acute posterior pointed spine, their surfaces smooth with fine pits. The telson is approximately as broad as long, its longitudinal margins with a fine beading; on the inner edge of the beading there is a smooth groove, then a ridge.

Appendages. On the large first cheliped the width of the palm is from three quarters to equal to the length; the inside face of the palm is flatly convex, the outer face half round; the inner edge is flattened along its length and the margin is armed with two rows of alternating teeth, five on the outer, four on the inner, the last on the joint margin; the outer margin is half round; the palm is smooth with fine pits of various sizes. A flat surface develops on the outer edge, extending to the full width at the base of the fixed finger, continuing parallel with the margin and becoming more noticeable on the outer face; it is about a third or more of the width of the fixed finger. The inner margin of the fixed finger is wide, almost flat, and armed with depressed oval teeth of varying size that lie close together. From the base of the fixed finger are three or four transverse



TEXT-FIG. 3. *Homarus morrиси* sp. nov., reconstruction of carapace ($\times 1.2$).

oval teeth of approximately the same size though their height gradually increases. These are followed by a larger oval raised tooth (greater length along the median line) and two much smaller oval teeth. The dactylus is about as long as the palm, its outer margin half round with a spine on the outer edge by the base. The outer surface is lightly rounded with a spine by the joint, paired to one on the palm. The inner surface is nearly flat with a similar spine to that on the outer surface. The prehensile edge is armed with one large oval tooth followed by three others diminishing in size towards the front, then a large rounded one followed by several smaller rounded ones.

On the small claw the palm is nearly as wide as long, the top and bottom surfaces convex. The inner margin has nine spines in two rows, the last on the margin of the joint with the dactylus. The outer margin is slightly flattened. The surfaces are smooth with fine pores, except for a spine on each surface at the joint with the dactylus. Only the base of the dactylus was preserved, oval in cross-section with a single spine on the outer margin at the joint, armed with fine spiniform teeth on the prehensile edge.

Discussion. Bell (1858, p. 39) comparing BM 59136 (pl. 9) with *H. belli* remarked 'that it more nearly approximates the common lobster and would probably be a distinct species'. It is now considered that this specimen and a large majority of the lobsters from the Isle of Sheppey are *Homarus*. The larger lobsters from this locality though well preserved are usually found in a crushed or flattened state, leading to distortion of the grooves. This makes identification difficult; where claws are preserved a spine can usually be found at the base, on the outer edge of the dactylus.

As well as the London Clay sites, the Barton Beds of Christchurch Bay have produced several large specimens of *Homarus* since the first recorded specimen (SM C7742) was collected by H. Keeping (Gardner *et al.* 1888). These specimens are thought to have originated from Horizons A3 and F. Due to the crushed state of the carapace where present, identification is difficult; so far only small pieces of the prehensile edges of the claws have been preserved; the pieces that do exist, though much larger, are apparently *H. morrissi*.

The Thanet Beds of Herne Bay have also produced specimens of *Homarus*, though only one has the remains of the prehensile edge and parts of the claws. These, together with the specimens from the Bracklesham Group of Bracklesham and Whitecliff Bay, are also apparently *H. morrissi*. It is appropriate to include these specimens with *H. morrissi* until better preserved material can be found to prove or disprove this statement. The Barton material known to date is: SM C7742; BM In.60905; piece of limb, JC Collection; BA/103-106, JSQ Collection. Herne Bay material: specimen collected D. Kemp, JC Collection. Bracklesham Bay material: BM In.29208 collected E. Williams. Whitecliff Bay material: W88, 117, and 123, JSQ Collection.

H. morrissi is similar to *H. gammarus* (Linné) and *H. americanus* Milne-Edwards, living members of the genus from Europe and America. It has a similar flattened edge on the outer margin of the propodus; the rostrum is dentate and downturned and the carapace grooves and spines are in

EXPLANATION OF PLATE 64

Figs. 1 and 2. A small specimen of the Recent lobster *Homarus gammarus* (Linnaeus). 1, lateral view of the carapace, $\times 1.5$. 2, claw showing spines on the outer margin of the dactylus and palm, $\times 1.75$.

Figs. 5 and 7. *H. morrissi* sp. nov., London Clay, Bognor Regis. 5, crusher claw, BM In.63364, $\times 1.3$. 7, fine claw, showing arrangement of spines on the outer margin of the dactylus and palm, BM In.63365, $\times 1.2$.

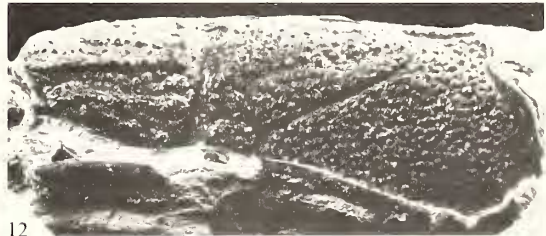
Figs. 3, 4, 6, 10. *Hoploparia gammaroides* M'Coy, London Clay. 3, crusher claw, OUM L558, Aveley, $\times 1.4$. 4, third maxilliped, BM In.63356, Maylandsea, $\times 2.2$. 6, lateral view of carapace, BM In.63354, Aveley, $\times 1.5$. 10, arrangement of spines (only one of the two rows is visible) on the palm; the base of the dactylus is smooth, OUM L563, Aveley, $\times 1.7$.

Figs. 8 and 9. *H. victoriae* sp. nov., Bracklesham Group, Lee-on-the-Solent. 8, lateral view of carapace, BM In.63357, $\times 1.8$. 9, prehensile edge of fixed finger crusher claw, showing the arrangement of the teeth (base only preserved), BM In.63363, $\times 2.5$.

Fig. 11. *H. wardi* sp. nov., London Clay, Chalk Farm, lateral view, SM C19318, $\times 1.25$.

Figs. 12-14. *Glyphea scabra* (Bell), London Clay. 12, lateral view of the holotype, BM 59146, Chalk Farm, $\times 2$. 13 and 14, left and right lateral views of BM In.63366, Aveley, $\times 2.3$.

Specimens in figs. 3, 5-8, 11, 13, and 14 have been whitened with ammonium chloride.



similar positions. It differs in that the inner margin of the palm has a double row of spines with the last at the joint margin. *H. gammarus* and *H. americanus* have a single row with the last spine before the joint margin.

H. davisi Stenzel, 1945 from the Cretaceous, Dallas Co., Texas, has a dentate carina running back from the antennal spine and a line of tubercles on the posterior edge of the postcervical groove; *H. morrissi* has neither of these characters. *H. brittonestris* Stenzel, 1945, also from the Cretaceous, Dallas Co., Texas, has a dentate rostrum and an antennal ridge followed by a small spine. The carapace is covered with tubercles, the largest over the gastric region and on top of the ridges in the vicinity of the rostrum. *H. morrissi* differs from *H. brittonestris* in having fewer rostral spines, no antennal ridge, and a finely pitted carapace.

H. hakelensis (Fraas) from the Cenomanian shale, Mount Lebanon, Syria, was provisionally placed in this genus by Glaessner (1945, p. 702). Due to the crushed state of these specimens it is difficult to make any valid comparison.

Genus HOPLOPARIA M'Coy, 1849

Type species. *Hoploparia longimana* (Sowerby), 1826, Upper Greensand, Lyme Regis, by subsequent designation (Rathbun 1926a, p. 129).

Diagnosis. Rostrum dentate, cervical groove clearly developed above and below the gastro-orbital groove, postcervical groove distinct, connecting with cervical groove through a semicircle; chelae strong, long, heterochelous.

Range. Lower Cretaceous-Middle Eocene.

Hoploparia gammaroides M'Coy, 1849

Plate 64, figs. 3, 4, 6, 10; text-fig. 2b, c

1849 *Hoploparia gammaroides* M'Coy, p. 177.

1849 *Hoploparia belli* M'Coy, p. 178.

1858 *Hoploparia gammaroides* M'Coy; Bell, p. 38.

1858 *Hoploparia belli* M'Coy; Bell, p. 39, pl. 10, figs. 1-3, 5-8.

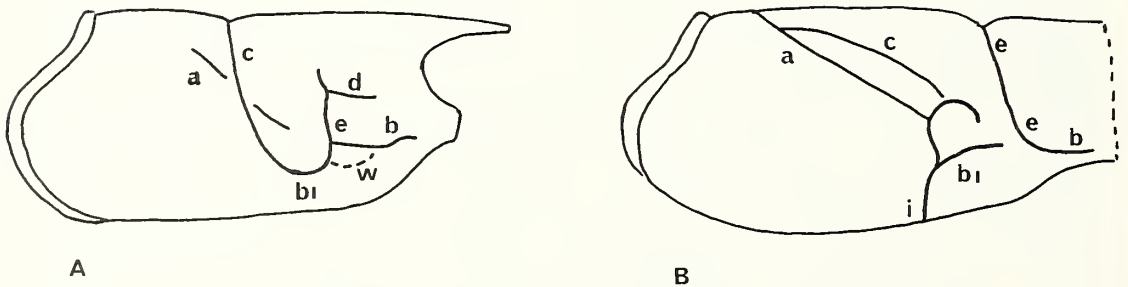
1929 *Hoploparia gammaroides* M'Coy; Glaessner, p. 219 (see for intermediate synonymy).

1931 *Homarus gammaroides* (M'Coy); Woods, p. 93, pl. 26, figs. 5 and 6; pl. 27, figs. 1, 2, 4.

1974 *Hoploparia gammaroides* M'Coy; Cooper, p. 85.

1980 *Hoploparia gammaroides* M'Coy; Morris, p. 9.

Types. M'Coy based his description on specimens at the University of Cambridge and the Bowerbank Collection, which should now be in the Sedgwick Museum and the British Museum (Natural History). No figure was given or reference made to identifiable specimens. In order to select a type for *H. gammaroides*



TEXT-FIG. 4. Carapace grooves. A, *Hoploparia* sp. ($\times 1.3$). B, *Glyphea scabra* (Bell) ($\times 2.0$). Identification of grooves: a, branchiocardiac; b1, hepatic; b, antennal; c, postcervical; d, gastro-orbital; e, cervical; ω , prominence omega; i, inferior.

both of these collections were carefully examined for a specimen that M'Coy could have used in his original description. It is almost certain that this description was based on material of more than one genus, i.e. *Homarus* and *Hoploparia*. No suitable specimen was found in the Sedgwick Museum and only one possible specimen in the British Museum (Nat. Hist.). This specimen, BM 46366 (Bowerbank Collection), has the characters of the species and was collected from the London Clay, Isle of Sheppey. Due to the uncertainty that M'Coy used BM 46366 (text-fig. 2*b, c*) for his original description of *H. gammaroides*, however, it is here designated the neotype.

Other material. The following specimens have been used as a basis for the description. OUM L461, L558 (Pl. 64, fig. 3), L559, L560, L563 (Pl. 64, fig. 10), L564, all *ex* Kirby Collection; BM In.63354 (Pl. 64, fig. 6), *ex* King Collection; BM In.63355–In.63356 (Pl. 64, fig. 4), *ex* JSQ Collection.

Diagnosis. A *Hoploparia* with the cervical joining the antennal groove at an obtuse angle; the antennal region prominent but without spines; posterior edge of the postcervical groove bordered with a line of fine granules; prominence omega, small and obscure, surface with fine tubercles.

Horizon and locality. London Clay, Lower Eocene of Aveley, Chalk Farm, Copenhagen House, Isle of Sheppey, Maylandsea, and Steeple.

Description. Cephalothorax. The median line on the rostrum is flanked by carinae, with a shallow depression between. The postorbital spine is below but almost level transversely with the start of these carinae. The rostrum is half the length of the carapace; its outer edges converge towards the tip. Approximately half-way along the rostrum a large, anterodorsally pointing spine projects on either side of the margin. A similar but larger spine projects on either side at about three quarters the length of the rostrum which then continues almost straight and parallel sided. At the second pair of spines the shallow depression has almost died out.

The cervical groove is deep, starting almost level with the suborbital spine and dropping nearly straight down with a very slight forward angle to join the antennal groove at an obtuse angle, turning towards the front and continuing straight until below the antennal region where it turns sharply anteriorly. At the junction of these grooves and the hepatic groove is a small obscure area known as the prominence omega. The distinctive broad postcervical groove runs from the median line slightly more than half the distance from the base of the rostrum to the posterior margin of the carapace. It slopes forward to the level of the antennal groove to join the hepatic groove. This is semicircular and joins the cervical groove. The hepatic groove starts strong, weakens towards mid length, then becomes stronger. At the top of the cervical groove a faint gastro-orbital groove runs towards the front. The branchiocardiac groove is evident faintly on some specimens, running backwards and upwards from the cervical groove at the level of the suborbital spine. A further faint furrow extends downwards from the postcervical groove at the level of the base of the orbit. The frontal and orbital regions are finely punctate; the antennal has fine tubercles and the odd pit; the branchial has regular spaced, fine and larger tubercles with some fine pitting towards the posterior margin; the gastric has scale-like pits on the top half, and tubercles on the bottom half; the cardiac is strongly pitted. (Refer to text-fig. 4 for position of grooves.)

Abdomen. The first abdominal somite is the smallest, the tergum with a transverse smooth groove, the raised portion pitted. The lateral margin of the pleuron is straight and finishes in a forward pointing, flat, blunt, tooth which overlaps the posterior edge of the carapace. The second somite has a transverse groove on the anterior third of the tergum, extending down to form a semicircle on the pleuron; the surfaces are smooth in front of the groove on the tergum, variably pitted behind. The pleuron is broadly quadratic, the anterior angle rounded, the posterior angle extended into a spine; between the lateral and the posterior margins is a large deep pit; surfaces are ornamented with fine pits, with some areas nearly smooth. The third and fourth somites have a transverse groove on the anterior third which extends to the boundary of the tergum at the anterior margin; surfaces are smooth in front of the groove, pitted behind. The pleuron is triangular, falcate, with an acute posteriorly directed spine. A weak semicircular groove starts and finishes at the pleuron boundary; below this groove and on the median line is a large pit; surfaces are variably pitted. The fifth somite is slightly smaller. The sixth is almost as deep as the second, with a groove crossing the tergum, which is pitted, near the anterior edge. The pleuron is triangular with an acute spine. A weak semicircular groove, which is a continuation of the tergum groove, finishes at a small spine on the posterior edge at the pleural boundary.

Telson. The telson is longer than broad, the outer margins converging slightly towards the rear. On each side of the median line a rounded ridge extends posterolaterally from near the front to a posteriorly pointing spine at slightly over three quarters distance along the margin. Beyond this the margin is semicircular, the surfaces

finely pitted. The endopodite is nearly as broad as long, the posterior margin well rounded, the sides converging towards the front to form a well-rounded margin. A longitudinal ridge diverges slightly from the median line on the inner side of the endopodite; there are fine tubercles on the ridge and the outer side; the inner side away from the ridge is smooth; the posterior quarter is finely ribbed at right angles to the margin. The exopodite is elliptical, nearly twice as long as broad and divided transversely by a suture at approximately two thirds of its length. The posterior margin of the anterior section is armed with a series of spines, the largest on the outer angle; the surface is finely punctate. The bottom third is finely ribbed, parallel with the median line, its surface finely punctate.

Appendages. Antennae long, reaching nearly as far forward as the outstretched first pair of pereopods. Antennal peduncle slightly more than one third the carapace in length, the three segments round to oval in cross-section and more or less equal in length to one another. On the first section of the peduncle the outer edge is flattened to form a sharp ridge which develops into a forward pointing spine. Jutting out in front of this first section and above the spine can be seen the remains of the antennal scale on some specimens. Pieces of the antennule peduncle can be seen on BM In.63354, length approximately to the end of the second section of the antennal peduncle.

The third maxilliped is approximately two thirds the length of the carapace. The merus is triangular in cross-section, its outer margin rounded; the lower margin has small evenly spaced pores; surfaces are finely punctate. The propodus is slightly longer than the carpus, both more or less oval in cross-section. The dactylus is spear shaped, flattened, approximately the same length as the carpus.

On the right-hand cheliped, the crusher, the outer margin of the propodus is rounded, with a faint suggestion of a lateral groove immediately inside the margin on either surface. The margin is smooth with lines of variable sized pits running along the fixed finger on the outer and inner surfaces. The fixed finger is oval in cross-section near the tip, changing to half round by the base of the finger, the inner surface nearly flat; a median triangular ridge runs along the length of the fixed finger. At the base of the ridge and running parallel to it is a line of pits; the remainder of the surface is ornamented with fine pitting. The ridge of the finger is armed with various sized teeth; from the base there are three oval blunt teeth of similar size, then a large blunt oval one (greater diameter along the median line); these are followed by groups of fine teeth divided by a slightly larger tooth. The palm is slightly shorter than the finger, and half as wide as long, nearly oval in cross-section; it thins rapidly near the inner margin to form a lateral groove on either surface. The inner margin of the palm has three large triangular spines on the outer edge, with a smaller spine behind the posterior tooth. Slightly away from the lateral line of spines but parallel with it are two similar spines on the under surface. These alternate with the previous spines. The dactylus is oval in cross-section, slightly flattened on both surfaces, the outer margin rounded. The prehensile edge is armed with a large oval tooth (the greater diameter along the median line), a smaller tooth separated by a gap from a large round tooth, then an assortment of large, fine and slightly larger teeth.

On the fine or left-hand claw, the outer margin of the propodus is smooth and round, straight for most of the length with a slight curve inwards at the tip, the surfaces with fine pitting. The fixed finger is nearly oval in cross-section towards the tip, half round in cross-section at the base; a triangular ridge on the median line runs along the prehensile edge, with fine spines or teeth in groups of three or four with a slightly larger spine in between. This sequence is repeated until approximately one third the length from base where there is a large, slightly offset spine followed by groups of fine and slightly larger spines. A line of pits runs parallel to the ridge; surfaces have variable pits. The finger is at least one and a half times the length of the palm, which is approximately half as wide as long. The outer surface of the palm is deeply convex, starting to flatten out near the inner margin. The inner surface is not as strongly curved. The inner margin is armed with three similar sized triangular spines with a smaller spine behind; parallel with these is another line of two or three similar spines on the under surface, alternating with the previous spines. The dactylus is almost oval in cross-section, flattened slightly on both surfaces, the outer margin rounded, the prehensile edge with a triangular median ridge on the top of which are groups of three or four spiniform teeth, with a slightly larger one in between. The carpus is nearly as broad as long with various anteriorly directed spines on the top and the margins, the underside with an anteriorly directed spine at the front, the surfaces variably pitted. The merus is half the length of the large claw, flattened to oval in cross-section, the front outer margin drawn out into a long sharp point with a smaller spine on the inner margin. Only pieces of the ambulatory legs are preserved; these are rounded to oval in cross-section, smooth with fine lines of pores or isolated pits; the second pair is chelate.

Discussion. When M'Coy (1849) established *Hoploparia* he included two new species from the London Clay, *H. gammaroides* and *H. belli*. Bell (1858) maintained both species but Woods (1931)

found that the smaller specimens (*H. belli*) differed in no significant respect from the larger (*H. gammaroides*) and united the two. A study of the original material confirms the view of Woods.

Bell (1858, p. 40) noted that *H. belli* (= *H. gammaroides*) appears to resemble *H. longimanus* (Sowerby) of the Lower Greensand. The latter has a line of tubercles behind and parallel with the postcervical groove, which in *H. gammaroides* are finer (Pl. 64, fig. 6). The junction of the antennal and the cervical groove is at an obtuse angle in both. The ornamentation of the carapace is quite different. *H. longimanus* has spines or tubercles on the carinae and a dentate carina runs back from the antennal spine towards the cervical groove. In *H. gammaroides* this area is prominent but without tubercles; it can vary in individuals as do some of the other surface decorations. *H. stokesi* (Weller, 1903) from the Lower to Middle Campanian, James Ross Island, is similar to *H. longimanus*, the main differences being in the carapace grooves, greater spinosity, and the proportions of the cephalothorax (Ball 1960, p. 12). The American species *H. tennesseensis* Rathbun, 1926*b* from the Upper Cretaceous, Ripley Formation, has a deep groove along the outer margin of the propodus and a row of three spines on the inner side of the inner margin, with one spine at the proximal end of the outer side of this margin. *H. gammaroides* has a double row of spines but arranged differently and no groove along the outer margin of the propodus. *H. gammaroides* differs from the above mentioned Cretaceous species in that the prehensile edge of the claw is armed differently.

Several Eocene species of *Hoploparia* are known, some only from pieces of claw. *H. klebsi* Noetling, 1885 from Germany has a row of spines running back from the antennal spine; the rostrum carinae running back on to the carapace are dentate. The inner margin of the palm of *H. klebsi* is armed with forward pointing teeth as well as the outer margin of the dactylus (Förster and Mundlos 1982, fig. 2). *H. gammaroides* differs from this species by having a prominent antennal region without spines; the prehensile edge of the claw and the inner margin of the palm are armed differently. *H. groenlandica* Ravn, 1903 from the Eocene of Kap Dalton, East Greenland has the cervical joining the antennal groove at an obtuse angle as in *H. gammaroides*. The hepatic groove is distinct throughout its length, and two dentate carinae run from the base of the rostrum nearly to the cervical groove. The chelae of *H. groenlandica* appear to differ from those of *H. gammaroides* in having a flat area on the inner and outer margins, but this may be preservational. Ravn (1903, p. 119) noted that this species has a greater resemblance to *H. gammaroides* though he relied on Bell's (1858) description and figures to come to this conclusion. The specimens are now assigned to *Homonarus* and *Hoploparia wardi* sp. nov. The hepatic groove of *H. gammaroides* is not distinct throughout its length; the rostral carinae are not armed and finish almost level transversely with the postorbital spine. These characters make *H. gammaroides* different from *H. groenlandica*. *H. corneti* van Straelen, 1921 from the Eocene of Belgium is too poorly illustrated (van Straelen 1921, p. 136) for any detailed comparison with other species.

Hoploparia wardi sp. nov.

Plate 64, fig. 11; text-fig. 2*d*

- 1849 *Hoploparia gammaroides* M'Coy, p. 177.
 1858 *Hoploparia gammaroides* M'Coy; Bell, p. 38, pl. 8, fig. 4.
 1858 *Hoploparia belli* M'Coy; Bell, p. 40, pl. 10, fig. 9.
 1931 *Homonarus gammaroides* M'Coy; Woods, p. 93, pl. 27, fig. 3.
 1980 *Hoploparia gammaroides* M'Coy; Morris, p. 9.

Derivation of name. Named after Mr David Ward.

Types. Holotype: SM C19314 (text-fig. 2*d*), Forbes Young Collection, London Clay, Isle of Sheppey. Paratypes: SM C19318 (Pl. 64, fig. 11), Walton Collection, and BM 59132*B*, Wetherell Collection (Bell 1858, pl. 10, fig. 9), London Clay, Chalk Farm; BM 46356, Bowerbank Collection (Bell 1858, pl. 8, fig. 4; Woods 1931, pl. 27, fig. 3), London Clay, Isle of Sheppey.

Diagnosis. A *Hoploparia* with a prominent carina running back from the antennal spine with two, possibly three tubercles and a further one between the nearly parallel postcervical and the cervical

grooves; distinct hepatic groove throughout its length; prominence omega triangular with fine tubercles; carapace ornamented with well-spaced fine tubercles, more closely spaced ventrally.

Description. Cervical groove deep, runs anteroventrally to join the antennal groove which curves gently anteriorly (rest of groove not seen). The distinct postcervical groove starts on the median line and runs anteroventrally to join the semicircular hepatic groove which joins up with the cervical groove. The hepatic groove is distinct throughout its length. Between the postcervical and the cervical grooves and in line with the cheek, is a swollen area capped with a prominent tubercle. Antennal region elevated into a strong keel with two, possibly three, tubercles. Carapace ornamented with variably sized fine tubercles, rear margin with a smooth flange. First abdominal somite traversed by a smooth groove, surface anterior of groove smooth with fine pitting behind. Somites two to four have a transverse groove on the anterior third which extends to the boundary of the tergum at the anterior margin; surfaces are smooth in front of the groove, with fine pitting behind which appears to increase in size and quantity from the tergum boundary downwards.

Discussion. In Bell's (1858) redescription of *H. gammaroides*, he quoted a sentence from M'Coy's original description: 'the cheek is elevated into a strong keel with about three large spinose tubercles; cheeks prolonged as a semi-cylindrical sheath to the outer antennae half the length of the rostrum.' Bell noted that he had not observed this structure, yet his figure 4 on plate 8 clearly shows a tubercle above the hepatic groove. The specimen (BM 46356, Bowerbank Collection) plainly shows a tubercle above the hepatic groove, with the cheek elevated into a strong keel, with two, possibly three, spinose tubercles. As regards the cheeks, it is quite possible that on the specimens available the antennal peduncle was fragmentary; it could then be mistaken as a continuation of the cheek. Bell also noted p. 41 that BM 59132b (pl. 10, fig. 9) differed in some respects from *H. belli*.

Rathbun (1935, p. 61) used four incomplete specimens to describe *H. johnsoni* from the Lower Eocene, Sucarnoochee Bed, Midway, Alabama. It has at least one spine on the lateral ridge leading to the rostrum and the antennal ridge is weakly defined (Rathbun 1935, pl. 14, figs. 27 and 28). *H. wardi*, though similar to *H. johnsoni*, is different in that it has a pronounced antennal ridge, smooth carinae from the rostrum, and a different arrangement of the larger carapace tubercles. *H. wardi* differs from its near neighbour *H. gammaroides* by the arrangement of the spines leading towards the antennal spine, the deep and clearly defined hepatic groove, and the postcervical and cervical grooves which run parallel and closer together. The prominence omega is triangular and ornamented with fine tubercles on both of these species. In *H. klebsi* the postcervical and cervical grooves appear to be parallel similar to *H. wardi* (Förster and Mundlos 1982, pl. 33, fig. 3) but in *H. wardi* the carina from the rostrum is smooth and the large carapace tubercles are different. In *H. groenlandica* the postcervical and cervical grooves are not parallel but diverge dorsally as for *H. gammaroides*, whereas in *H. wardi*, the postcervical and cervical grooves run parallel and the carapace is ornamented with several large tubercles.

Hoploparia victoriae sp. nov.

Plate 64, figs. 8 and 9

1979 *Hoploparia gammaroides* M'Coy; Quayle and Collins in Kemp *et al.*, p. 102.

1981 *Hoploparia gammaroides* M'Coy; Quayle and Collins, p. 735.

Derivation of name. After my daughter, Miss Victoria Quayle.

Types. Holotype: BM In.63357 (Pl. 64, fig. 8). Paratypes: BM In.63358–In.63363 (Pl. 64, fig. 9), all *ex* JSQ Collection, from Unit 7, Elmore Formation, Bracklesham Group, Middle Eocene, Lee-on-the-Solent, Hampshire.

Diagnosis. A *Hoploparia* with the cervical joining the antennal groove in a curve; prominence omega well rounded and conspicuous, plain or pitted surface; antennal region rounded but not prominent; posterior border of postcervical groove plain or pitted.

Description. *Cephalothorax.* The rostrum is half the carapace in length, with a median depression bounded on each side by a carina; at approximately the mid length is the base of a spine and at the end a further spine (the

arrangement of the spines is possibly as for *H. gammaroides*). The cervical groove is deep, extending ventrally from the level of the suborbital spine, forming a smooth curve to join the deep antennal groove. The antennal groove becomes finer towards the anterior margin of the carapace, where it almost disappears. At the junction of these grooves and the weak hepatic groove is a small, prominent well-rounded area, the prominence omega. The hepatic groove alongside this area is smooth, wide, and deep, but elsewhere, even on well-preserved specimens, is very indistinct. A weak furrow extends anteriorly from the top of the cervical groove, passing under the suborbital spine. The postcervical groove is deep, situated at over half the carapace length from the base of the rostrum. The dorsal part cuts the median line at right angles and runs anteroventrally approximately 30° to the vertical to join up with the hepatic groove. A further deep furrow extends ventrally from the postcervical groove at the level of the base of the orbits. The branchiocardiac groove curves posterodorsally from the cervical groove, at the level of the suborbital spine. The marginal furrow is well marked and the posterior margin bears a smooth, finely punctate flange. Surface ornamentation on the carapace is as follows: frontal and orbital area, smooth with well-spaced pits; antennal area, pitting with small tubercles; branchial area, blunt tubercles with pits; gastric and cardiac areas, surface rough with pitting.

Abdomen. The tergum of the first abdominal somite is crossed by a deep groove two thirds the distance from the front; raised portions are pitted. A groove crosses the tergum of the second somite in the anterior third and extends down to form a semicircle on the pleuron. The pleuron is quadrate, the anterior angle rounded, the posterior angle with a posterior pointing spine. Between the bottom of the semicircle and the posterior spine is a large clear pit; the rest of the surface is ornamented with variable pitting. The third somite is likewise traversed by a groove which extends to the pleuron, where it forms a weakly defined semicircle. The pleuron is falcate, with an acute posteriorly pointed spine, its surface ornamented with variable pits, the area in front of the tergum groove smooth. Somite four is similar to three; the groove on the pleuron is very weak, the pleura having a solitary pit similar to that on somite two. The fifth somite is like three and four but narrower, its surfaces variably pitted.

Ventral surfaces. There is a median tubercle on the abdominal sterna of the first to third somite. Mandibles are almost rectangular, smooth and transversely convex with other surfaces and margins rounded.

Appendages. On the right-hand first cheliped, the crusher, the palm is approximately twice as long as wide, oval in cross-section, thinning rapidly towards the inner margin which has two rows of alternating, anteriorly directed spines (six in all?). The palm is coarsely pitted. The fixed finger is nearly oval in cross-section, its outer margin rounded with a slight groove on the upper surface, its inner margin wide, almost flat. From the base of the fixed finger the prehensile edge is armed with depressed oval teeth that lie close together with their greater length at right angles to the median line. The first tooth is the smallest with a marked increase in size to the third; then the teeth remain almost the same size up to the tenth (rest not seen). The dactylus (of which only fragments are known) is oval in cross-section, its outer margin wide and flat, the prehensile edge armed with close, round to oval, flattened teeth, smallest at the joint. On the upper and lower surfaces a spine is evident by the joint. On the left-hand first cheliped, the small claw, the palm is approximately twice as long as wide and oval in cross-section. It thins rapidly towards the inner margin which is dentate with a double row of alternating spines. The fixed finger has a rounded outer margin, the inner margin almost flat for its entire width, the prehensile edge armed with small spiniform teeth for most of its length. The carpus is approximately two thirds the length of the merus, triangular in cross-section, its inner and outer margins tapering towards the merus. The lower surface has a row of three or four anteriorly directed spines. The upper surface is slightly rounded with an anteriorly directed spine towards the rear. Ornamentation on the upper surface is scale-like. There are small blunt tubercles on the lower surface. The merus is over twice as long as wide, oval in cross-section, its inner and outer margins tapering from the front towards the ischium. There are one or two blunt spines on the anteroventral margin; surfaces are smooth, finely punctate. The ischium is smooth and finely punctate. On the second and third pereopods the merus and ischium are round and smooth with surfaces finely punctate; the merus is approximately three times the length of the ischium.

Discussion. *H. victoriae* differs from *H. gammaroides* in that the antennal and cervical grooves join in a curve; the posterior edge of the postcervical groove is plain or with pits; the antennal region is rounded on the surface and only prominent at the front; prominence omega rounded with plain or pitted surface; the prehensile edge of the propodus of the crusher claw is armed with oval teeth increasing in size away from the joint and transverse to the median line. *H. victoriae* differs from *H. wardi* and *H. klebsi* in that the cervical and postcervical grooves are further apart and diverge

dorsally, and in the carapace ornamentation, small tubercles with fine pitting. It differs from *H. groenlandica* in that the rostral carinae are smooth.

Infraorder PALINURA Latreille, 1803
Superfamily GLYPHEOIDEA Winckler, 1883
Family GLYPHEIDAE Winckler, 1883
Genus GLYPHEA von Meyer, 1835

Type species. *Palinurus regleyanus* Desmarest, 1822, by original designation.

Diagnosis. Carapace with short pointed rostrum; tuberculate longitudinal carinae on anterior part. Cervical groove deep and steeply inclined in lateral view. Postcervical and branchiocardiac grooves very oblique, joined medially and laterally and in some species at additional points. Anterior portion of carapace rectangular in dorsal and lateral views. Branchiostegite with long narrow anterior extension. Abdominal terga smooth, telson rounded, exopods of uropods with diaeresis. Antennal scale pointed; first pereiopod subchelate.

Range. Upper Trias-Lower Eocene.

Glyphea scabra (Bell, 1858)

Plate 64, figs. 12-14; text-fig. 5b

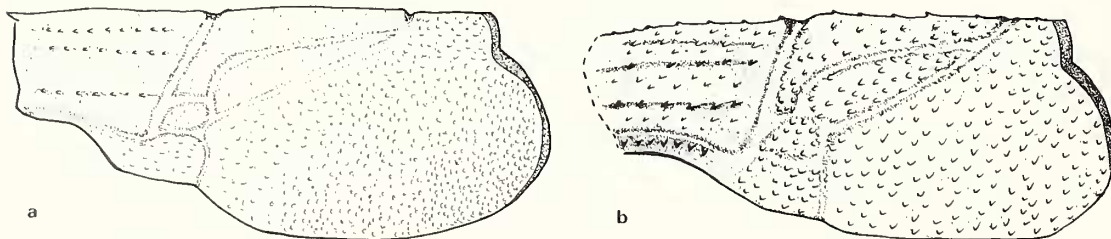
- 1858 *Trachysoma scabrum* Bell, p. 41, pl. 10, fig. 11.
- 1929 *Trachysoma scabrum* Bell; Glaessner, p. 387.
- 1930 *Trachysoma scabrum* Bell; Woods, p. 73, pl. 22, fig. 1a, b.
- 1969 *Trachysoma scabrum* Bell; Glaessner, R464.
- 1974 *Trachysoma scabrum* Bell; Cooper, p. 85.
- 1980 *Trachysoma scabrum* Bell; Morris, p. 17.

Holotype: BM 59146 (Pl. 64, fig. 12), by monotypy, London Clay, Chalk Farm, Camden Town, London.

Other material. BM In.63366 (Pl. 64, figs. 13 and 14), collected by D. Ward, London Clay, Aveley, Essex; PE 80/454, collected S. W. Vincent, A127 (roadworks) at Folkes Lane, Cranham (TQ 580 884).

Diagnosis. A *Glyphea* with the carapace covered in different size sharp pointed tubercles.

Description. Cervical groove deep, starting at a point about two fifths the distance from the front to the posterior margin of the carapace. It runs nearly straight, until half-way across the carapace where it bends slightly forward and continues to the antennal groove. In front of the cervical and above the antennal groove are three longitudinal carinae armed on the top with sharp anteriorly directed tubercles; the surfaces between the carinae are ornamented with further sharp tubercles. The antennal groove is deep, nearly straight with a slight upwards angle. The branchiocardiac groove is clearly marked. It starts at approximately four-fifths the distance from the front with a slight forward curve, then runs almost straight across the carapace at an angle of 45° to meet the small lobe above the hepatic lobe. The indistinct postcervical groove forms an acute angle with the branchiocardiac groove near the dorsal margin; anteriorly the grooves are joined by a semicircle and a triangular area is formed between them. The hepatic groove starts at the junction of the branchiocardiac



TEXT-FIG. 5. a, *Glyphea* sp. ($\times 1.5$). b, Reconstruction of *Glyphea scabrum* (Bell) ($\times 2.2$).

and inferior grooves, runs slightly anterodorsally from this junction, then ventrally before joining the cervical groove above the antennal groove. The area bounded by the hepatic, inferior groove and the lower margin is roughly rectangular and decorated with sharp tubercles. The remainder of the surface of the carapace is also ornamented with tubercles.

What may be part of the propodus is evident on BM In.63366 (Pl. 64, fig. 13). It is oval in cross-section, the top margin with anteriorly directed equally spaced teeth, the outer surface with a smooth groove running parallel with the top margin; all surfaces with tubercles. (Refer to text-fig. 4B for position of carapace grooves.)

Discussion. Bell (1858) described the new genus *Trachysoma* from one specimen collected by Wetherell, to which he gave the trivial name *scabrum*. The holotype consists of an incomplete carapace with limb fragments and part of the antennal peduncle. Bell (p. 42) was not certain of the affinities of this species. Woods (1930) figured this unique specimen (pl. 22, fig. 1a, b) but gave no description or remarks. Cooper (1974) mentioned a specimen collected by D. Ward, BM In.63366. This consists of an imperfect carapace with a limb fragment. The only other known specimen (PE 80/454), part of a carapace, was collected by S. Vincent. Glaessner's (1969) diagnosis of *Trachysoma* refers to a long, low and narrow carapace with deep straight cervical grooves, and straight postcervical and branchiocardiac grooves. He also included *Glypheopsis* Beurlen in this genus, the type of which is *Orphea ornata* Quenstedt, 1858. This appears to have straight postcervical and branchiocardiac grooves (R465, fig. 269.2a, b). BM 59146 and BM In.63366 have had little or no preparation since being collected. What appears to be the rounded ventral margin of the carapace on BM 59146 is in fact a limb lying across the carapace. Likewise what appears to be a dentate ventral margin forward of the cervical groove is in fact a line of sharp tubercles. Both of these specimens were masked by matrix in a similar position which concealed the true shape of the carapace, which preparation of BM In.63366 has subsequently revealed, though details of the rostrum and anterior are still not known. A new reconstruction based on these specimens (text-fig. 5b) shows that the carapace compares in its proportions and grooves to *Glyphea* (text-fig. 5a) to which it is here assigned.

Superfamily PALINUROIDEA Latreille, 1803

Family PALINURIDAE Latreille, 1802

Genus ARCHAEOCARABUS M'Coy, 1849

Type species. *Archaeocarabus bowerbanki* M'Coy, 1849, London Clay, Isle of Sheppey, by original designation.

Diagnosis. Rostrum of moderate size made up of three spines, centre one gripped by two processes of the ophthalmic somite; supraorbital spines widely separated. Sternal plate with four pairs of tubercles.

Range. Lower Eocene, England.

Discussion. Woods (1931) diagnosed *Archaeocarabus* as like *Palinurus* but with the rostrum similar to that of *Jasus* Parker, 1883, particularly in that it is gripped by two processes of the ophthalmic somite. He distinguished it from *Jasus* by the more widely separated supraorbital spines and the presence of a row of tubercles on the plastron. The differences in the rostral area between *Jasus* and *Archaeocarabus* can be seen by comparing text-fig. 6C with text-fig. 6D. In *Archaeocarabus* there are three spines; in *Jasus* a single central spine. The rostrum or central spine in each case is gripped by two processes of the ophthalmic somite. These two processes in *Archaeocarabus* tend to lie alongside the spine with a slight upwards curve, rather than come straight up from the ventral side as in *Jasus*.

Archaeocarabus bowerbanki M'Coy, 1849

Plate 65, figs. 1-9; text-fig. 6

1849 *Archaeocarabus bowerbanki* M'Coy, p. 174.

1854 *Archaeocarabus bowerbanki* M'Coy; Pictet, p. 443, pl. 42, fig. 3.

1858 *Archaeocarabus bowerbanki* M'Coy; Bell, p. 42, pl. 11, figs. 1-5.

- 1925 *Archaeocarabus bowerbanki* M'Coy; Woods, p. 36, pl. 8, fig. 5; pl. 9, fig. 6; pl. 10, figs. 1-3.
 1929 *Archaeocarabus bowerbanki* M'Coy; Glaessner, p. 57.
 1962 *Archaeocarabus bowerbanki* M'Coy; Roberts, p. 176.
 1969 *Archaeocarabus bowerbanki* M'Coy; Glaessner, R473, fig. 277.2a, b.
 1974 *Archaeocarabus bowerbanki* M'Coy; Cooper, p. 85.
 1980 *Archaeocarabus bowerbanki* M'Coy; Morris, p. 1.

Types. M'Coy's syntypes are SM C7737, C7738, C19074, BM 46358, 46359, and 59764, all from the London Clay, Isle of Sheppey. SM C7737 (Woods 1926, pl. 9, fig. 6) is here designated lectotype.

Other material. BM 38388 (Pl. 65, fig. 6) and 59140 (Pl. 65, fig. 8); BM In.63378 (Pl. 65, fig. 5), In.63379 (Pl. 65, fig. 4), In.63380 (Pl. 65, figs. 1 and 3), In.63381 (Pl. 65, fig. 2), In.63382 (Pl. 65, fig. 9), In.63383-In.63386 (Pl. 65, fig. 7), *ex* JSQ Collection; all from the London Clay, Isle of Sheppey.

Diagnosis. As for genus.

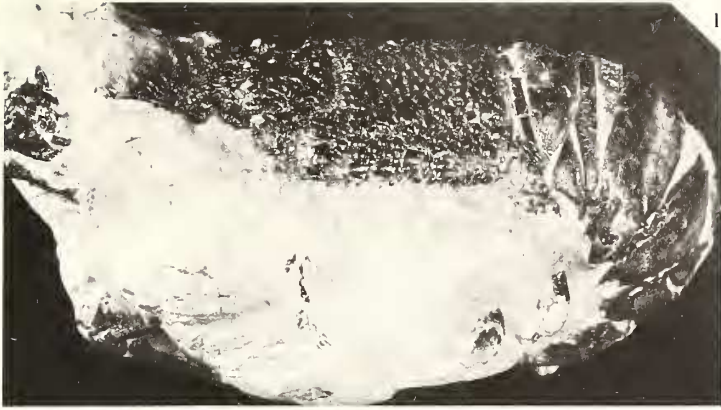
Description. Cephalothorax. The front is straight and occupies nearly half the carapace width; it is armed with several anteriorly directed spines. Length of the rostrum is two thirds of its width and occupies approximately a quarter of the width of the frontal margin; it consists of a thin median spine with a slightly shorter stout lateral spine either side. The median spine is armed dorsally with one anteriorly directed spine at approximately half the length, with a further spine at the base; lateral spines, broad at the base, are flat and triangular; the median spine is gripped on either side by two slightly upturned rounded cone-shaped processes of the ophthalmic somite. The somite is slightly wider than the rostrum; its outer margins are angled inwards; the top surface is concave and the sides drop steeply away; surfaces are smooth with a few small pits. The remainder of the front is made up of three short spines on either side of the rostral spines, followed by the supraorbital spines. These are large, anteriorly directed, laterally compressed and triangular in shape and lean slightly outwards; they are approximately half the carapace width in length and are situated at the anterolateral angle. Behind each runs the postorbital carina; this is cut by the cervical groove and continues behind with a slight inwards angle, gradually dying out and ending three quarters of the length of the carapace from the front. On the carina there are two smaller, anteriorly directed spines behind the supraorbital spine and behind these, large spiny tubercles are interspersed with smaller ones. Between the supraorbital spines the carapace is almost flat with a few small tubercles. Half the distance from the front to the postcervical groove there is a transverse row of three small tubercles. Behind this and on either side of the mid-line are two longitudinal rows of three larger, anteriorly directed spines; from the second tubercle to the postcervical groove the general ornamentation of the carapace changes to a greater number of tubercles.

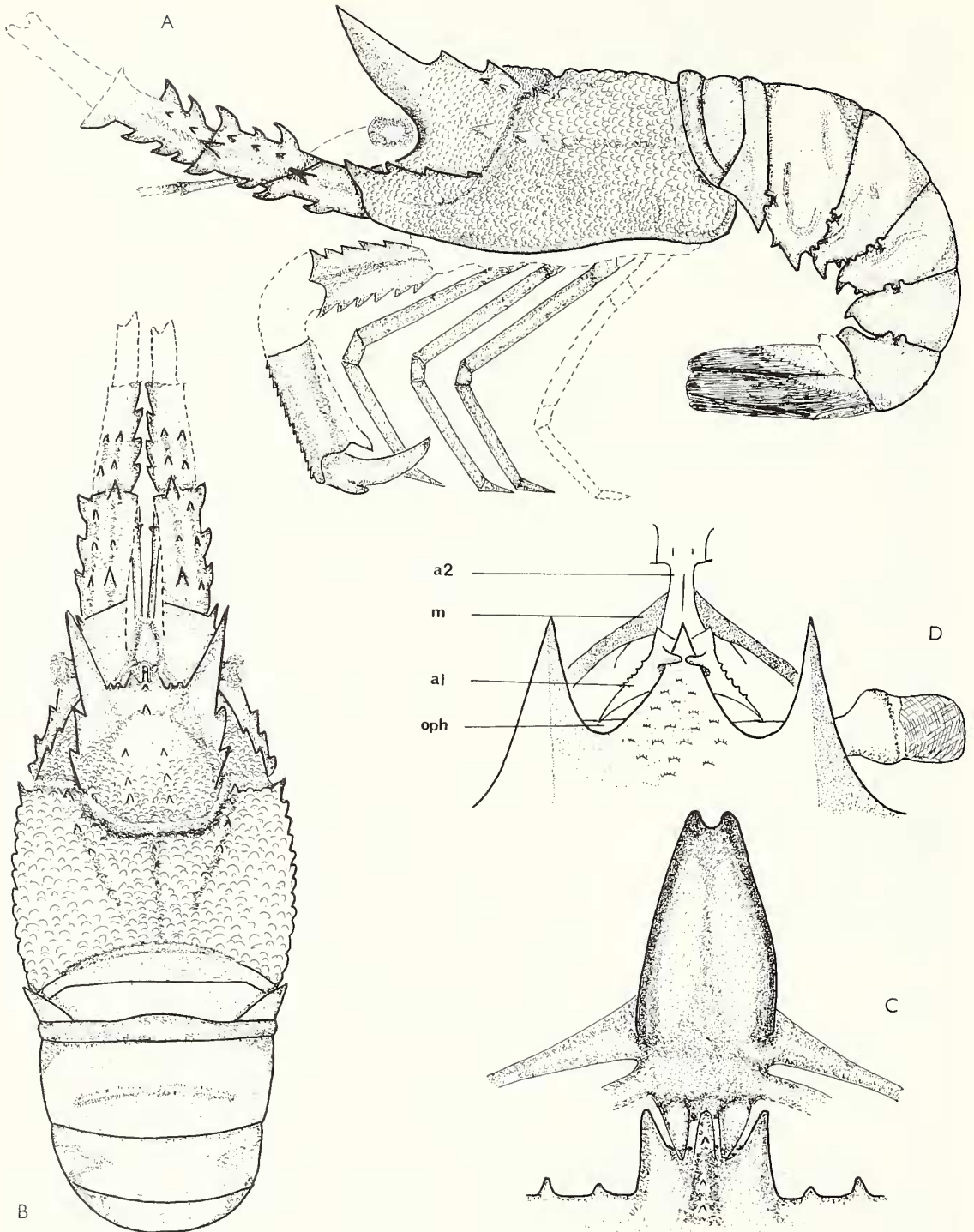
The postcervical groove is deep and broad, straight for half the width of the carapace, then joining the cervical groove which curves in front of the fourth spine on the continuation of the postorbital carina; it continues to run straight to cut the lateral margin at right angles, drops vertically down the side as a deep groove, then develops a slight forward curve which continues as the antennal groove. Behind the postcervical groove a slight median carina with large and small tubercles runs almost to the posterior margin where it is cut by a deep transverse groove, parallel to and just inside the flanged edge of the posterior margin. The lateral margins behind the cervical groove are parallel and start with a large forward pointing spiny tubercle, followed by four or five smaller spiny tubercles to half-way along the margin; a more general ornamentation then develops of small and large tubercles. The rest of the carapace is ornamented with a variety of medium and small tubercles. The large and small tubercles have on their front sides rows or groups of fine pores at the base. Below the supraorbital spine the orbital margin finishes in a large triangular infraorbital spine similar to but not as large as the supraorbital. Here starts the antennal carina which runs parallel to the postorbital carina and finishes at the antennal groove; it is armed with three flattened anteriorly directed triangular spines. At a point half-way between the carinae and alongside the cervical groove is the start of another carina that

EXPLANATION OF PLATE 65

Figs. 1-9. *Archaeocarabus bowerbanki* M'Coy, London Clay, Isle of Sheppey. 1 and 3, BM In.63380. 1, lateral view, $\times 1.1$. 3, dorsal view, $\times 1.1$. 2, eye and orbit, BM In.63381, $\times 2$. 4, basal segments of antenna, BM In.63379, $\times 1.7$. 5, ophthalmic somite, BM In.63378, $\times 4$. 6, anterior of BM 38388, $\times 2$. 7, lateral view, BM In.63386, $\times 0.8$. 8, sternum, BM In.59140, $\times 1$. 9, claw, BM In.63382, $\times 1.8$.

Specimens in figs. 3, 5, and 9 have been whitened with ammonium chloride.





TEXT-FIG. 6. *Archaeocarabus bowerbanki* M'Coy, diagrammatic reconstruction. A, B, lateral and dorsal view ($\times 1.1$). C, details of the ophthalmic somite and rostrum ($\times 3.6$). D, *Jasus lalandii* (Milne-Edwards), Recent, South Africa, frontal area (after Glaessner 1969) ($\times 1.25$): a2, base of antenna; m, articulating membrane; a1, antennular base; oph, eye stalk.

forms the continuation of the lateral margin posterior to the cervical groove, which dies out before the orbital margin and is armed with two or three blunt spines. There are a further two, anteriorly directed triangular spines between this carina and the postorbital carina at the forward edge of the cervical groove.

Abdomen. On the abdominal somites the tergum is more or less semicircular in cross-section, with a grooved and flanged posterior margin. The pleura have one to three flat spines on each margin and end in a large recurved central spine. On the first somite the flange develops a triangular flap on each side, which accommodates the posterolateral angles of the carapace when the abdomen is rolled up. The surfaces are variably pitted.

Telson. The calcified part of the telson is parallel sided, with the posterior margin concave; there are a few tubercles towards the centre. Approximately the first half of the outer margin of the exopodite and endopodite is calcified. This area is elliptical, approximately three times longer than wide, smooth on the outer edge, strongly serrate on the inner and terminates in a ventrally directed spine. Only fragments of the remainder of the tail are known.

Ventral structures. The anterior margin of the epistome is concave on each side of the median spine and reached by the median furrow. The anterior part of the sternum is a small rectangular area, a fifth of the total length; the outer margins then diverge to give the maximum width at the second sternite, which remains almost constant as far as the concave rear margin. Along the median line and on the rear margin of each sternite behind the rectangular area are pairs of tubercles. The first and last pair are smaller than the intermediate pairs. The surface of the sternum is finely granulated and decorated with tubercles on the outer margins.

Appendages. The long slender basal podomere of the antennule reaches as far forward as the end of the second podomere of the antenna. The basal podomere expands distally to accommodate the second slender podomere, only small pieces of which are preserved. The first three podomeres of the antenna are round to oval in cross-section and armed with various sized spines. The dorsal and ventral margins of the second and third podomeres are flattened slightly longitudinally, and armed with large flattened anteriorly directed triangular spines. The flagellum is unknown but was probably similar to Recent *Palinurus*. The eye is very large and the peduncle short, about one third the width of the eye.

The first pereiopod is chelate, the propodus three to four times the width of that on limbs two to five, but approximately the same length; in cross-section it is round to oval, becoming broadly dilated towards the dactylus; the width of this flattened end is two thirds the length of the rounded, slightly curving, outer margin of the pointed dactylus. On the outer margin, opposite the joint, is a large posteriorly directed spine. There are two or three longitudinal rows of uniform pits on the outer and inner surfaces, with the odd larger pit. On the second, third, and fourth pereiopods the merus is slightly longer than the propodus. Both are oval to triangular in cross-section. The merus is smooth and finely punctate; the propodus has longitudinal lines of small evenly spaced pores; the rest of the surface is finely punctate. The dactylus is slightly less than half the length of the propodus, round in cross-section, with a pointed end.

Discussion. Due to the very fragile nature of the carapace of *Archaeocarabus*, it is rarely found complete; BM In.63380 (Pl. 65, figs. 1 and 3), though small, is possibly the best preserved. The carapace of the larger specimens appears to be more rounded, with the carinae becoming indistinct.

Rathbun 1935 described two new species of *Archaeocarabus*? and in 1945, a further one. Roberts (1962, p. 176) was doubtful whether these three species should have been placed in *Archaeocarabus*.

Genus LINUPARUS White, 1847

Type species. *Palinurus trigonus* von Siebold, 1824, by original designation.

Diagnosis. Cephalothorax depressed, carapace with three longitudinal keels, no rostrum; supra-orbital spines close to the median line, fused to form plate or separated by indentation.

Range. Lower Cretaceous–Recent.

Discussion. Three species of Recent *Linuparus* were recognized by Berry and George (1972): *L. trigonus* (von Siebold), 1824, western Pacific, Japan, South China Sea, Philippines, and eastern Australia, *L. sordidus* Bruce, 1965, from the South China Sea to north-western Australia, and *L.*

somniosus Berry and George, 1972, from the western Indian Ocean, Mozambique, and Natal, living in depths from 81 to 328 m. There were variations in the type series of each, small specimens having better developed spines than large ones. As pointed out by Woods (1925) there are also variations in the fossil species.

Linuparus eocenicus Woods, 1925

Plate 66, figs. 1-5; text-fig. 7a, b

- 1858 *Thenops scyllariformis* Bell, p. 33, pl. 7, figs. 5?, 6, 7?, 8?
 1925 *Linuparus eocenicus* Woods, p. 31, figs. 3-5; pl. 7, figs. 4-6; pl. 8, fig. 1.
 1929 *Linuparus eocenicus* Woods; Glaessner, p. 233.
 1974 *Linuparus eocenicus* Woods; Cooper, p. 85.
 1980 *Linuparus eocenicus* Woods; Morris, p. 10.
 1980 *Linuparus scyllariformis* (Bell); Morris, p. 10.

Types. Woods's syntypes are SM C7732, C7733 (Pl. 66, fig. 3)-C7736, Meyer and Carter collections, from the London Clay, Portsmouth Docks, Hampshire; BM 59145, London Clay, Highgate tunnel, London. SM C7735 (Pl. 66, figs. 1 and 2) is here designated lectotype.

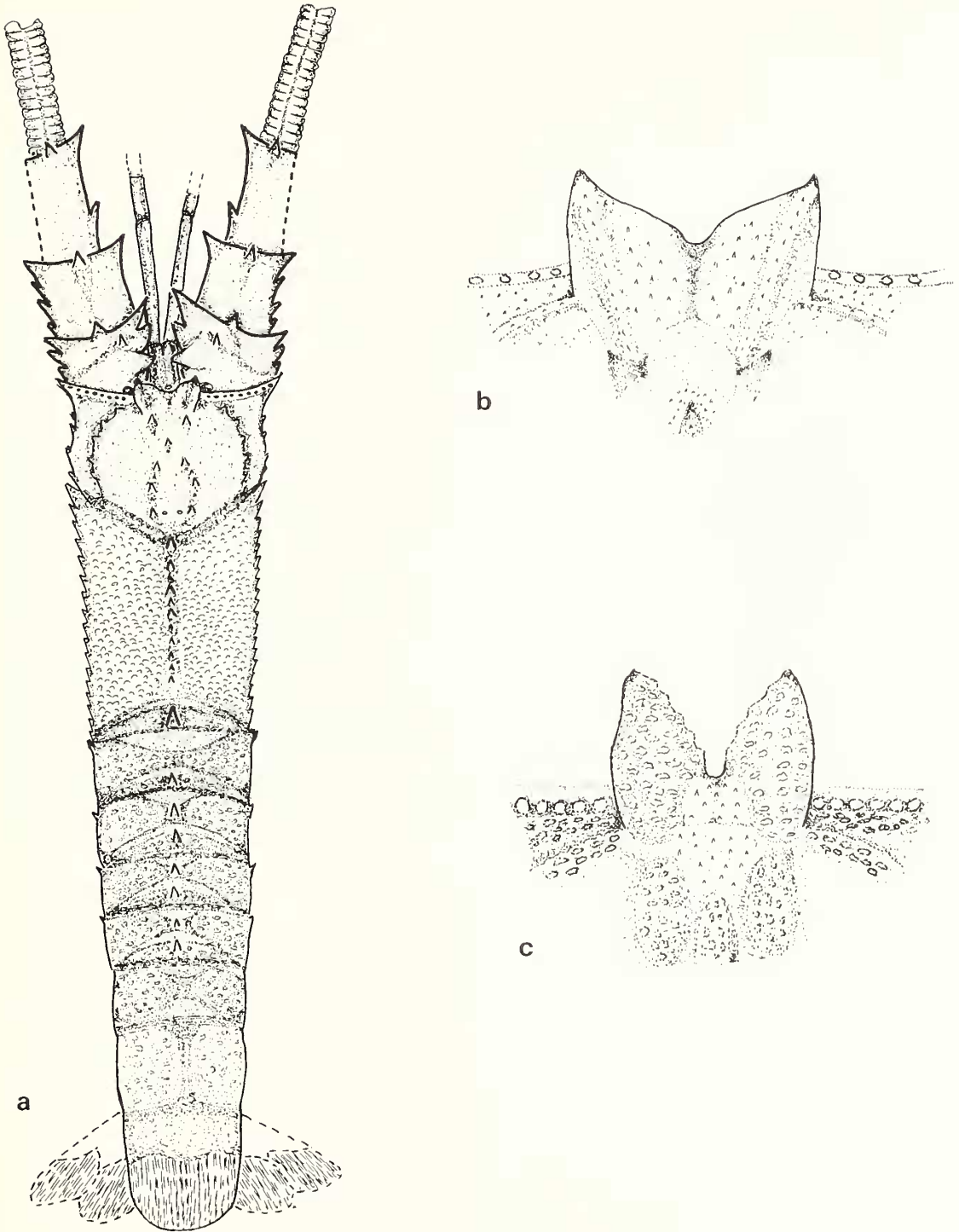
Other material. SM X1357-1362; OUM L552-L554, L568-L570; BM In.63370, In.63371 (Pl. 66, fig. 4)-In.63374 (Pl. 66, fig. 5) In.63377; all *ex* JSQ Collection, Whitcliff Bay, Isle of Wight. The following of Bell's syntypes of *L. scyllariformis*: BM 59012, 59107-59109, 59111, 59141 certainly, and 46365, 46367, 59765, 59114, and 59110b probably, belong to *L. eocenicus*.

Horizon and locality. The London Clay of: Portsmouth Docks; Isle of Sheppey; Burnham on Crouch; Highgate and Chalk Farm, London; Frinton on Sea; Base of Division E, Barwell Court, Surrey; and the Wittering Division, Bracklesham Group, Whitecliff Bay.

Diagnosis. A *Linuparus* with the supraorbital spines united for half their length; carinae with spiny tubercles, raised areas decorated with fine tubercles.

Description. Cephalothorax. The supraorbital spines take up approximately one quarter the width of the frontal margin. They are ridged longitudinally, the outer margin sloping steeply away from the ridge. The inner margins, from the tip of the spine to the centre line where they meet, form a shallow U. They are united for approximately half their length. The frontal margin outside the supraorbital spines is concave, with well-spaced tubercles running along the top surface, and terminates in an anteriorly directed anterolateral spine. A short distance behind each supraorbital spine is a postorbital spine, which continues posteriorly as a ridge as far as a median spine. Behind this the median line is flanked by carinae, which diverge slightly and then converge meeting just anterior of the cervical groove; these carinae bear small anteriorly directed spines. In between these carinae almost at the cervical groove is a pair of small, deep, round pores, flanking the median line. From near the base of the supraorbital spines, rounded carinae extend outwards in a curve to the cervical groove and bear several forward pointing spines; the area bounded by these is concave. The raised surfaces are covered with fine tubercles; other areas are nearly smooth. External to the curved carina the carapace at first slopes sharply ventrally and then becomes nearly horizontal; surfaces are tuberculate. The lateral margin in front of the cervical groove is angular and bears several small anteriorly directed spines and usually one or two larger spines along its length; it is nearly parallel to the axis of the body. The cervical groove is deep and in the form of a shallow V. At the lateral margin the deep groove runs directly ventrally and then bends sharply anteriorly. Behind the cervical groove are three nearly parallel longitudinal carinae, the median prominent, the outer angular. Between the median and lateral carinae the carapace is flattened or concave and ornamented with regularly spaced uniform tubercles. Carinae are ornamented with numerous spines, usually decreasing in size towards the posterior. External to the lateral carina the carapace is vertical except near the cervical groove, where the upper part is concave and the lower convex. Just in front of the posterior margin of the carapace is a broad smooth groove which interrupts the median carina and curves backward on each side, becoming narrower towards the lateral margins. This part of the carina is produced into an anteriorly directed spine.

Abdomen. The abdomen is similar in length to the carapace, tapering slightly posteriorly. The carinae on the carapace are continued as slight ridges on each tergum. The first somite bears one anteriorly directed spine on



TEXT-FIG. 7. *a, b, Limparus eocenicus* Woods. *a*, diagrammatic reconstruction ($\times 0.7$); *b*, supraorbital spines ($\times 2.1$). *c, L. scyllariformis* (Bell), supraorbital spines ($\times 1.7$).

the median ridge at the posterior margin. In front of this a smooth groove runs almost parallel to the posterior margin for approximately half the width of the somite, where it divides. One arm runs to the posterior margin at the outer edge, the other to the outer edge near the front of the somite; the two triangular areas enclosed are ornamented with some fine tubercles and pits; the area in front is smooth. Somites two, three, and four have a median carina, which is interrupted in the middle of each tergum by a broad transverse groove, sloping posteriorly on each side, narrowing and nearly reaching the posterior margin. The tergum surface is ornamented with a mixture of pits and fine tubercles. Each tergum has two anteriorly directed spines on the median carina, one in front and one behind the groove; on the outer margins there is a suggestion of a longitudinal ridge with a spine at the front. On the fifth somite the spines on the median ridge have disappeared, but the outer spine is still evident with the transverse groove becoming indistinct. The sixth somite, which is almost twice the length of the others, has a smooth median groove with a longitudinal row of tubercles on each side; the rest of the surface is ornamented with fine tubercles. The pleura on somites four and five bear two spines on the forward margin followed by a central ventrally directed strong spine. The posterior margin is smooth laterally becoming serrate, the size of teeth increasing adaxially; a concave area flanks the central spine. Only parts of the pleura of somites two and three are known but they are presumably as for four and five.

Ventral structures. The epistome has a strong median groove between prominent ridges which diverge anteriorly. The anterior margin is concave with a tubercle either side of the median groove. The anterolateral margins are directed at approximately 45° to where they turn posteriorly and become almost parallel. Between the margins and the two median ridges are two large depressions, one alongside each ridge.

The sternum between the third maxilliped and the first pair of pereopods is triangular and bears two flat, rounded bosses anteriorly, one behind the other; surfaces are pitted. The coxae of the third maxillipeds fit between these bosses. Each sternite has ridged sides tapering towards the front, decorated with pits and tubercles. The lateral and posterior margins join in a triangular, laterally directed spine. The sternite for the first pereopod is ridged along the median line; the second, third, and fourth have a large tubercle either side of this line. The fifth has two pairs of small tubercles, one pair either side of the median line; the outer ridge is smooth except for some tubercles towards the front. Between the tubercles on the sternite for the fourth limb is a groove along the median line. There is a single central tubercle on the first abdominal somite. On the second there are three tubercles, the two anterior approximately half the size of the posterior one. On the third somite the three tubercles are in a similar position to the second but are all the same size with a smaller tubercle in between the pair. The fourth and fifth have a pair of tubercles, one either side of the median line.

Appendages. The antennular somite is longitudinally rectangular with a broad median furrow and it extends forward between the basal podomere of the antennae. The basal podomere of the antennule is round and thin, extending past the second podomere of the antenna. The first podomere of the antenna is broad and one third wider than the second. The outer and inner margins are sharp and armed with two or three forward pointing spines. The second podomere is similar in length to the first; the third is the longest, but also the narrowest.

The coxa of the third maxilliped is triangular, its surfaces pitted. The merus is approximately half the size of that on the second pereopod; surfaces nearly smooth with very shallow pits. The first pereopod is larger than the rest, the coxa nearly as long as the ischium and basis, surfaces with shallow pitting. The merus, three times as long as the carpus, is flattened and forked at the carpus articulation with sharp spines on the ventral margins by the fork; the propodus is half the length of the merus. Other limbs are similar but the fifth appears to be smaller.

Discussion. Of the three Recent species of this genus *L. trigonus* is the nearest to *L. eocenicus*. On *L. trigonus* the supraorbital spines have a dentate inner margin; the frontal margin has a prominent spine half-way between the supraorbital and the anterolateral spine. On *L. eocenicus* the supraorbital spines have a smooth inner margin and there is no prominent spine on the frontal margin. Possibly the arrangement of the spines on the pleura is different.

The fossil species are known from the Cretaceous and the Eocene. *L. canadensis* (Whiteaves, 1885), Northwest Territory, Highwood River, Alberta, has two spines on the tergum boundary whereas *L. eocenicus* has one. *L. vancouverensis* (Whiteaves, 1895) from the Nanaimo Group, Vancouver and Hornby Islands, British Columbia, has a double row of tubercles on the carapace carinae (Rathbun 1935, pl. 10, figs. 1-3); the carapace carinae continue back on to the tergum as ridges armed with a single row of tubercles. In *L. adkinsi* Rathbun, 1935 (pl. 10, figs. 4-10) from the Denton Clay, Texas, the three carinae behind the cervical groove are granulated, the median

one with a double row of tubercles. The tergum has a pronounced median carina with a series of tubercles. *L. eocenicus* bears a single row of tubercles on the carapace carinae which continue back on to the tergum as a ridge with a single or double spine.

The English Cretaceous has produced *L. carteri* (Reed, 1911) from the Lower Greensand, Atherfield, Isle of Wight. The cervical groove starts as in other species of the genus but forms an obtuse angle where it becomes transverse just before it crosses the median line; from this obtuse angle a further groove runs backwards. In addition the arrangement of the tubercles on the carinae and the general ornamentation of the carapace (Woods 1925, pl. 7, figs. 2 and 3) differentiate this species from other members of the genus.

The Eocene members of the genus include *L. texanus* Rathbun, 1935 (pl. 16, figs. 9 and 10) from the Midway of Dimmit County, Texas. It is possible that this species, which was described from one specimen, is not distinct. Rathbun (1935) described the abdomen as lacking the first and second segments: it is suggested that these are really segments one to five and not three to seven. The median spine on all the specimens of species examined is lost on the fifth segment with a groove appearing on the sixth, which does not appear to happen in this case. *L. wilcoxensis* Rathbun, 1935 (pl. 16, figs. 11-14) from the Sucarnoochee Beds, Wilcox County, Alabama, appears to be very similar to *L. eocenicus*. The abdomen has two spines on the median carina on segments two to four with possible differences on the outer carinae of these segments.

Woods (1925, p. 32, pl. 7, fig. 6b) described the antennular somite of *L. eocenicus* as triangular. On closer examination the sides of the 'triangle' are seen to be chipped or broken and in recently collected specimens it is evident that this somite is long and parallel sided, with a deep median furrow (Pl. 66, fig. 5).

Linuparus scyllariformis (Bell, 1858)

Plate 66, figs. 6-8; text-fig. 7c

- 1858 *Thenops scyllariformis* Bell, p. 33, pl. 7, figs. 1-4.
- 1925 *Linuparus scyllariformis* (Bell); Woods, p. 29, pl. 8, fig. 2a, b.
- 1929 *Linuparus scyllariformis* (Bell); Glaessner, p. 233.
- 1974 *Linuparus scyllariformis* (Bell); Cooper, p. 85.
- 1980 *Linuparus scyllariformis* (Bell); Morris, p. 10.

Types. Bell's syntype BM 59106, figured Woods (1925, pl. 8, fig. 2), London Clay, Whetstone, London is here designated lectotype. Of the paralectotypes BM In.43325, BM 59110a, 59113, 59142, 59143 certainly and 59144 probably belong to *L. scyllariformis*.

Other material. OUM L265, L460, L462 (Pl. 66, fig. 8), L555 (Pl. 66, fig. 6), Kirby Collection; BM In.63367-In.63369, ex JSQ Collection; PE 82/395 collected C. King.

Horizon and locality. The London Clay of: Herne Bay, Aveley, Maylandsea, Steeple, Whetstone, Felixstowe, and roadworks on the M25, Ockendon Road, approximate grid reference TQ 565 926.

Diagnosis. A *Linuparus* with large separate pyriform supraorbital spines, with prominent pits as surface decoration on ridges and spines.

Description. *Cephalothorax.* Large separate pyriform supraorbital spines on either side of the median line are divided by a deep U-shaped depression. The frontal margin runs slightly concave outwards from near the base of these spines to end in a prominent anteriorly directed anterolateral spine. The dorsal surface along the frontal margin bears evenly spaced blunt tubercles; the front edge of the margin is at right angles to the dorsal surface and is smooth except for rare fine tubercles, which tend to increase in number towards the anterolateral angle.

Directly behind and in line with the supraorbital spines are blunt postorbital spines, which continue back in the form of rounded ridges; between and parallel to these is a small rounded median ridge, separated by a small gap from a rounded tubercle at the front. Posterior to this, there is on each side a rounded carina. These diverge slightly almost as far as the cervical groove where they converge enclosing a flat area. From near the base of the supraorbital spines rounded carinae extend outwards in a curve to the cervical groove. These

carinae are ornamented with two or three blunt tubercles. External to these carinae the carapace slopes vertically, then becomes nearly horizontal as far as the lateral margin where it slopes steeply again and begins to curve inwards. The lateral margin is slightly concave for one third the length from the anterolateral spine to where it erupts into another prominent forward pointing spine, beyond which it curves inwards to the cervical groove. The carapace in front of the cervical groove is ornamented with numerous pits on the spines, ridges, tubercles, and carinae, whilst the flat or concave areas are nearly smooth with fine tubercles. The cervical groove is deep. Behind it are three parallel longitudinal carinae, of which the median one is prominent; the carapace between the median and the lateral carinae slopes steeply away from the centre with a slight concavity until it reaches the outer margin. Just in front of the posterior margin of the carapace is a broad, smooth transverse groove, which interrupts the median carina and curves back on either side, becoming narrower towards the outer margins. The carapace behind the cervical groove is ornamented with fine equal-sized tubercles except for the carinae which are covered with pits.

Abdomen. The abdomen tapers slightly towards the tail. The carinae on the carapace continue as ridges on each tergum. The first somite has one anteriorly directed spine on the central ridge at the posterior margin. In front of this a groove runs almost parallel to the posterior margin for approximately half the width of the somite where it forks, one branch to the posterior margin at the outer edge, the other forward to the outer edge near the front of the somite. The two triangular areas enclosed by these branches are deeply pitted, whilst the area in front is smooth with very fine punctae. Somites two, three and four have two anteriorly directed spines on the central ridge of the tergum, separated midway by a deep transverse groove; this slopes back on either side to cut the outer ridge just in front of the posterior margin. On each of the outer ridges are two forward pointing spines, one in front, the other behind the groove. The tergum surface is deeply pitted, except the grooves which are smooth. The fifth somite lacks spines, and the posterior groove has almost disappeared. The sixth has a deep median groove with a prominent longitudinal line of pits on either side. The tergum of each somite is triangular in transverse section with a slight flattening towards the outer ridge.

Ventral surfaces. The epistome has a deep median furrow; anteriorly running parallel to this furrow is a large forward pointing blunt tubercle, the top surface of which has a line of several deep pits. The front edge of the epistome is concave with steeply sloping sides, ornamented with variably sized fine tubercles with some shallow pits.

Appendages. The antennular somite is longitudinally rectangular, with a deep, broad, median furrow extending forward between the basal segments of the antennae. The first podomere of the antennal peduncle has two forward-pointing spines on the outer edge; the top surface is coarsely pitted, the underside smooth, with fine well-spaced pits. The second podomere is nearly half the width of the first and has small spines on the outer edge. The third is smaller than the second with two spines on the inner margin. The flagellum is longitudinally grooved on the upper and lower surfaces.

On the third maxilliped the merus is two thirds the length of that on the first pereopod, its outer side flat, inner edge flattened, margin tuberculate, surfaces deeply pitted. The first pereopod is larger than the remainder. The merus is equal in length to the total length of the carpus, propodus, and dactylus, roughly oval in cross-section, flattening on the underside towards the front, the surface becoming concave; the inner margin is tuberculate, the surfaces decorated with small tubercles. The carpus is rectangular, flattened at the merus and increasing in depth towards the front (i.e. triangular in side view) and decorated with various sized tubercles. The propodus is slightly longer than the carpus, approximately oval in cross-section but slightly flattened, the surfaces with tubercles and pits. The dactylus, one third the length of the merus, is pointed distally; fragments of the inner margin show a line of large shallow pits with very fine pits inside these. Merus, carpus, and propodus of the second pereopod are similar to the first but smaller.

EXPLANATION OF PLATE 66

Figs. 1-5. *Limuparus eocenicus* Woods. 1-3, London Clay, Portsmouth Docks. 1 and 2, dorsal and ventral view of lectotype, SM C7735, $\times 1$. 3, lateral view, SM C7733, $\times 0.65$. 4 and 5, Bracklesham Group, Whitecliff Bay. 4, anterior, showing supraorbital spines, BM In.63371, $\times 0.7$. 5, antennular somite, BM In.63374, $\times 0.6$.

Figs. 6-8. *Limuparus scyllariformis* (Bell), London Clay. 6, dorsal view, OUM L555, Aveyley, $\times 1$. 7, ventral view, BM 59106, Whetstone, $\times 0.8$. 8, supraorbital spines, OUM L462, Aveyley, $\times 1$.

Specimens in figs. 1, 2, and 6 have been whitened with ammonium chloride.



QUAYLE, *Limparus*

Discussion. On the other species of this genus the carinae and ridges are usually dentate or tuberculate. *L. scyllariformis* differs in that the area in front of the cervical groove is ornamented with numerous pits on the spines, ridges, tubercles, and carinae, and behind this groove the carinae are covered with pits.

Family SCYLLARIDAE Latreille, 1825
Genus SCYLLARIDES Gill, 1898

Type species. *Scyllarus aequinoctialis* Lund, 1793, by original designation, Recent.

Diagnosis. Eyes near anterolateral angles; lateral margins of carapace without deep fissures, rostrum salient.

Range. Lower Cretaceous–Recent.

Discussion. Woods (1926, p. 41) says of *S. koenigi* (= *S. tuberculatus*) 'This species agrees so closely with living forms of *Scyllarides* and differs from that of *Scyllarus* that there seems no reason for retaining Bell's genus *Scyllaridia*' (1858, p. 35). Holthuis (1954) proposed use of the Plenary Powers to render the name '*Scyllarides*' Gill, 1898 the oldest available for this species; *Scyllaridia* was suppressed by the International Commission (1954, Opinion 293, pp. 134–136). Glaessner (1969, R475) stated that 'if the fossil is not congeneric with the recent genus as claimed by Woods (1926), it must be given a new name'. However, the present author agrees with Woods that the fossil belongs to the Recent genus.

Scyllarides tuberculatus (König, 1825)

Plate 67, figs. 1–6

- 1825 *Cancer (Scyllarus?) tuberculatus* König, p. 3, pl. 4, fig. 54.
- 1843 *Cancer tuberculatus* König; Morris, p. 72.
- 1854 *Zanthopsis tuberculatus* König; Morris, p. 116.
- 1858 *Scyllaridia Koenigii* Bell, p. 35, pl. 8, figs. 1–3.
- 1870 *Scyllaridia Bellii* Woodward, p. 493, pl. 22, figs. 1 and 2.
- 1925 *Scyllarides koenigi* (Bell); Woods, p. 39, pl. 10, figs. 7–10.
- 1929 *Scyllarides koenigi* (Bell); Glaessner, p. 376.
- 1969 *Scyllarides? koenigi* (Bell); Glaessner, R475, fig. 281.3.
- 1974 *Scyllarides koenigi* (Bell); Cooper, p. 85.
- 1980 *Scyllarides tuberculatus* (König); Morris, p. 16.

Types. The holotype, by monotypy, is BM 42228 (Pl. 67, figs. 4 and 5), London Clay, Isle of Sheppey. Of Bell's figured specimens, syntypes of *S. Koenigii*, the original of pl. 8, fig. 1, is missing; pl. 8, fig. 2 is BM 59115 (Pl. 67, fig. 6) and fig. 3 is BM 46364, both from the London Clay, Isle of Sheppey.

Other material. OUM L566 (Pl. 67, figs. 2 and 3); BM In.63387–In.63389 (Pl. 67, fig. 1), ex JSQ Collection; all from the London Clay, Isle of Sheppey.

EXPLANATION OF PLATE 67

Figs. 1–6. *Scyllarides tuberculatus* (König), London Clay, Isle of Sheppey, Kent. 1, ventral view, BM In.63389, $\times 2.5$. 2 and 3, OUM L566. 2, somites four to six with calcified part of telson, $\times 1.4$. 3, lateral view, $\times 2.4$. 4 and 5, dorsal and lateral view of the holotype, BM 42228, $\times 1.2$ and 1.1 . 6, dorsal view, BM 59115, $\times 1.45$.

Figs. 7–9. *Bathysquilla wetherelli* (Woodward), London Clay, Isle of Sheppey, Kent. 7 and 8, BM In.63390. 7, fragments of carapace, thoracic somites six to eight, abdominal somites one to four, $\times 1$. 8, part of the raptorial claw, $\times 5$. 9, abdominal somites one to five, BM In.63391, $\times 2.3$.

Specimens in figs. 1–6 and 9 have been whitened with ammonium chloride.



Horizon and locality. The London Clay, Isle of Sheppey and Whetstone, London; derived material from the London Clay, Red Crag, Felixstowe, and Walton-on-the-Naze.

Diagnosis. A *Scyllarides* with carapace and ridges covered with various sized tubercles, a large spiny tubercle on the median carina and another between this and the cardiac carina.

Description. The following is not a full description but consists of additions or changes to that of Woods (1925).

Cephalothorax. The margin between the rostrum and the preorbital spine is concave and occupies one quarter the anterior width. The strong anterodorsally directed preorbital spine is the continuation of a longitudinal carina which runs parallel to the median line, broken by the branchiocardiac groove, and continuing nearly to the posterior margin. Between the preorbital spine and the branchiocardiac groove lies a small blunt tubercle. The orbit is well rounded and terminates on the anterior margin; its lower margin bears an anteriorly directed spine on the outer side; the orbits occupy approximately one quarter of the anterior margin. The remainder of the margin to the anterolateral angle is slightly concave. There is a strong forward pointing lateral spine at the anterolateral angle reaching slightly further forward than the rostrum. The postcervical groove cuts the median line at right angles at a point approximately half the distance from the rostrum to the rear of the carapace; it forms an obtuse angle with the cervical groove, which is directed anterolaterally.

Some of the carapace tubercles have groups or lines of fine pores, possibly for setae. Larger pores lie in front of the tubercles on the elevated gastric region and lateral margins. There are other small round holes or pits at various places on the carapace. The outer margin runs slightly inwards from the anterolateral angle to the niche for the cervical groove. There are several forward pointing small blunt spines on this margin. The remainder of the lateral margin runs almost parallel, with several anteriorly directed blunt spines.

Abdomen. On the tergum of abdominal somites two to five a deep transverse groove cuts the median line at one third the distance from the front and runs forward until it reaches the anterior margin, just above the tergum boundary. A carina is formed on the median line behind this groove. Approximately half-way down the tergum a slight groove starts at right angles to the main groove and continues roughly in a semicircle to the posterior margin at the tergum boundary. This groove encloses a raised area which continues on to the pleura. The anterior margin slopes from the median line vertically to the tergum boundary, where a hollow boss accommodates the cone-shaped tubercle on the posterior margin of the previous somite. The margin then curves gently towards the rear and forms a scythe-like ventral spine with the posterior margin. The posterior margin ventral to the cone-shaped tubercle is slightly convex with a serrate edge of five or six downward pointing blunt spines. At the last of these spines the margin becomes strongly concave to form the posterior edge of the ventral spine. The posterior margins of the terga of somites five and six bear posteriorly directed blunt tubercles or spines. On the tergum of the sixth somite there is an additional groove, with a rear margin with blunt tubercles, instead of a median carina. On the pleuron of the sixth somite the posterior margin is slightly more concave, almost semicircular, to accommodate the tail members. The surfaces of somites one to six have irregular sized pits, both deep and shallow.

Telson. The calcified part of the telson has blunt tubercles of various sizes with groups or rows of fine pores towards the rear; towards the lateral margins the ornament changes to small irregular pits.

Ventral surfaces. The sternum, which is triangular with a median groove, is evident between the first and fifth pair of pereopods. There is a pair of small tubercles at the front, flanking the median line, opposite the coxa of the first pereopod. This is followed by four pairs of large tubercles, flanking the median line and opposite the coxae of the succeeding pereopods. Between the last two pairs of tubercles on the median line is a round cavity. The posterior margin of the sternum is straight, the surfaces tuberculate on raised portions, smooth at the bottom of grooves.

Appendages. The coxae of the first to fifth pereopods are triangular. The basis and ischium have a combined length similar to that of the coxa. The merus is oval in cross-section with a longitudinal ridge and pitted surfaces.

Discussion. König (1825) described and figured a unique specimen (BM 42228, Pl. 67, figs. 4 and 5) from the London Clay of the Isle of Sheppey, to which he gave the name *Cancer (Scyllarus?) tuberculatus*. Bell (1858, p. 36) considered that 'the whole surface of the carapace is fictitious, and the very tubercles on which the name was found exist only in obedience to the skill and trickery of the artist', an opinion with which Woods (1925) largely agreed. As a result of his misinterpretation,

Bell disregarded König's name *tuberculatus* and substituted the honorific *Koenigi*. On examination by the present author, however, it became clear that this specimen consists of a normally preserved (i.e. with surface detail) abdomen of *Scyllarides* and an internal cast of the carapace. The general shape of the two tubercles on either side of the body as depicted by König (1825, pl. 4, fig. 54) is evident on the specimen. Bell's argument for changing the name of this species rested on the fact that he considered that the carapace surface and the tubercles were fictitious. König's original name is retained here, as advocated by Morris (1980).

Order STOMATOPODA Latreille, 1817
 Family SQUILLIDAE Latreille, 1803
 Genus BATHYSQUILLA Manning, 1963

Type species. *Lysiosquilla microps* Manning, 1961, by original designation, Recent.

Diagnosis. Telson with blunt median carina and all four pairs of marginal teeth with movable apices.

Range. Lower Eocene–Recent.

Bathysquilla wetherelli (Woodward, 1879)

Plate 67, figs. 7–9

- 1879 *Squilla wetherelli* Woodward, p. 549, pl. 26, fig. 1.
 1969 *Squilla? wetherelli* Woodward; Holthuis and Manning, R541.
 1974 *Squilla wetherelli* Woodward; Cooper, p. 85.
 1980 *Squilla wetherelli* Woodward; Morris, p. 17.

Type. The holotype, by monotypy, is BM 59780 (Woodward 1879, pl. 26, fig. 1), London Clay, Highgate, Wetherell Collection.

Other material. BM 38399 collected W. Griffith; BM In.38262 collected D. J. Jenkins; In.63390 (Pl. 67, figs. 7 and 8) and In. 63391 (Pl. 67, fig. 9), both ex JSQ Collection.

Horizon and locality. All from the London Clay: BM In.38262, Beltinge, East Cliff, Herne Bay; BM 38399, BM In.63390, and In.63391, Isle of Sheppey.

Diagnosis. A stomatopod with a marginal carina on the abdominal somites and a fine transverse groove on the tergum of the second abdominal somite; the propodus of the raptorial claw is armed with spiniform teeth.

Description. The posterolateral angle of the carapace is well rounded, and the posterior margin straight. The surface of the thoracic tergites curves steeply ventrally on either side of the median line in a regular curve to the lateral margin of the tergum where there is a slight ridge. The pleura of somites seven and eight have a deep U-shaped indentation in the lateral margin. The width of the somites increases slightly towards the telson, eight being the widest at approximately half the width of the first abdominal somite. Abdominal somites one to four curve steeply ventrally on either side of the median line in a regular curve to the lateral margin where there is a slight ridge which turns slightly inwards to form a semicircular depression on the pleuron. This depression varies in width and depth; on the second somite it is nearly the full width and half the depth of the pleuron but it decreases in size on successively posterior pleura. The remaining surface of the pleuron is almost flat. The posterolateral angle of each pleuron is produced backwards into a small acute tooth and the posterior margin is straight. Each somite (one to four) has an oblong punctum on either side near the lateral margin of the terga; somites two to four bear two small sub-central puncta on the anterior border; three and four have a single central punctum on the posterior border. A fine groove, approximately two thirds the width of the tergum in length, runs parallel to the posterior margin and cuts the median line of the second somite at mid-point. Part of the tergum of the fifth somite is preserved with a single central punctum near the posterior margin. The sixth somite has a scabrous surface ornamentation.

The remains of the raptorial claw are evident on BM In.63390 (Pl. 67, fig. 8). Part of the inner margin of the propodus is preserved showing four equally spaced spiniform teeth. The dactylus is almost complete; the inner margin bears at least seven strong triangular teeth increasing in size to the terminal one.

Discussion. The Recent members of this group are abundant but are mainly restricted to tropical and subtropical seas. The type species *Lysiosquilla microps* was described by Manning (1961, p. 693) from two Recent specimens taken from 732 and 916–952 m off the east and west coasts of Florida.

Fossil stomatopods are rare and usually imperfectly preserved. The oldest known, *Sculda* Münster, 1840 (Holthuis and Manning 1969, R541), occurs in the Jurassic lithographic limestones of Solenhofen, Bavaria. New material from the Eocene of the Isle of Sheppey shows that the species described here cannot be included in the genus *Squilla*. Some of the diagnostic characters are not preserved but the longitudinal carinae on the abdomen and the upper margin of the propodus, and the even pectination of closely placed short blunt spinules are absent. This species shows similarities to both *Harpiosquilla* Holthuis, 1964 and *Bathysquilla*. The first closely resembles *Squilla* and has spaced spiniform teeth on the upper margin of the propodus of the raptorial claw but in all species the abdomen is strongly carinate. *Bathysquilla* lacks carinae on the abdomen and the propodus of the raptorial claw is armed with spiniform teeth. The affinities of this species therefore lie with *Bathysquilla*.

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